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Adaptive Probing Strategies for Age-Structured Fish Stocks

D. LUDWIG AND R. HILBORN

Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C. V6T 1W5

LUDWIG, D., AND R. HILBORN. 1983. Adaptive probing strategies for age-structured fish stocks. Can. J. Fish. Aquat. Sci. 40: 559 – 569.

This paper examines methods of preventing a stock of fish from being held far below its optimal size. Such sustained overexploitation could arise because the model used to manage the stock poorly represented the stock dynamics, because there are significant errors in the estimates of stock abundance, or because there is insufficient contrast in catch and fishing mortality to generate reliable estimates of the productive potential of the stock. We develop a method to correct for biases due to errors in estimates of abundance and show that this correction does improve estimates of productivity, but not sufficiently to enable a manager to recognize the presence of overexploitation. We demonstrate that the management system must generate significant contrast in catch and effort, and once the contrast is generated the managers can easily find near optimal abundance of the stock. With reasonable levels of contrast even very simple surplus production models will perform well when managing complex age-structured fish stocks.

LUDWIG, D., AND R. HILBORN. 1983. Adaptive probing strategies for age-structured fish stocks. Can. J. Fish. Aquat. Sci. 40: 559 – 569.

On examine, dans l'article qui suit, les façons de prévenir le maintien d'un stock de poissons à un niveau inférieur à son effectif optimal. Une surexploitation continue pourrait résulter d'un modèle de gestion représentant mal la dynamique du stock, d'erreurs importantes dans les estimations d'abondance et, enfin, d'un contraste entre prises et mortalité par pêche trop faible pour donner des estimations fiables du potentiel productif du stock. Nous avons mis au point une méthode pour corriger les biais résultant d'erreurs dans les estimations d'abondance et montrer qu'en fait cette correction donne de meilleures estimations de productivité, sans pour cela permettre au gestionnaire de reconnaître une surexploitation. Nous démontrons que le système de gestion doit engendrer suffisamment de contraste entre prises et effort et qu'une fois ce contraste obtenu, les gestionnaires découvriront facilement l'effectif quasi optimal du stock. Avec des niveaux de contraste raisonnables, même de très simples modèles de production excédentaires donneront de bons résultats dans la gestion de stocks de poissons à structure par âge complexe.

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MANY of the world's fisheries are overfished — they could support considerably higher harvests if fishing pressure were reduced for a period of time sufficient to allow recovery of the stock. The dramatic recovery of stocks such as the B.C. herring (Hourston 1981), Bristol Bay sockeye, the Pacific halibut between 1920 and 1940, and the North Pacific fur seal suggest that recovery policies may be effective. These policies were prompted by a recognition that the stock was overexploited, and this was largely established in the examples by the fact that previous harvest had been much higher, and indices of population size such as catch per unit effort, spawning counts or indices, had declined.

Essentially all methods used to assess stock abundance are dependent upon a documented record of variable exploitation of a stock: Gulland's method (1961) depends upon a knowledge of the fishery as it develops. Similarly, methods which attempt to determine productivity per unit stock or biomass as a function of stock size (Schnute 1977) rely upon sufficient variability in stock size to detect the numerical relationship between stock and production (Hilborn 1979). Even detailed measurements of fishing mortality (F) versus natural mortality (M) depend upon having a period of low F in order to estimate M. This means that large stock sizes must have been observed to know that the stock is currently overexploited.

There are at least three reasons why a useful historical record may not exist for a current fishery that is possibly overexploited. First, the data collection system may not have existed during the development of the fishery; for example, what is now commercially valuable may have been discarded as non marketable by-catch in past years. Second, with the fishing potential of today's fishing fleets, many fisheries can be developed from a virgin condition to overexploitation in a few years. Finally, a wider recognition that fish species interact with their ecosystems and that these ecosystems change over time, has led many fisheries scientists to question whether the data collected during the slow development of a fishery are reflected in the current productive potential of a stock. The failure of the California sardine (Marr 1963) emphasizes dramatically how past data may not be relevant today.

Given these three problems, we believe that many fisheries may be possibly overexploited, and no examination of the historical record will be sufficient to resolve the question. In principle, the biomass dynamics models such as Schaefer (1954) should be sufficient to detect overexploitation, since the relationship between stock and production at low densities should be linear (show no compensation). However, Hilborn (1979) showed how management methods based on Schaefer type models generally fail to detect an overexploited fishery, and the recent work of Ludwig and Walters (1981), Walters and Ludwig (1981), and Uhler (1980) provides good evidence that, given errors in measurement of spawning stock, compensation may appear due to these errors, and it is almost impossible to detect a true stock recruitment relationship. This means that it may appear as if there is compensation in data from an overexploited fishery even if there is none.

In this paper we present a method to remove the intrinsic bias in spawner recruit data taken from catch and effort time series, and show that this is generally insufficient to determine if a stock is overexploited. We then develop a formal method of experimental fisheries design to determine if a stock is overexploited, and provide a recovery policy for such fisheries.

Our analysis uses catch per unit effort as a measure of abundance, but our results are in fact much more general. They apply to any management system that relies on a measure of abundance that is measured with error, be it echosounding or experimental fishing.

The Estimation Scheme

We shall employ a nonlinear catch−effort relationship:

$$(1)\quad C_t = N_t(1 - \exp(-qe_t)).$$

Here C_t denotes the observed catch at time t,
N_t denotes the population (biomass) at time t,
E_t denotes the observed effort at time t,
e_t denotes the effective effort at time t,
q denotes a "catchability" coefficient,
S_t denotes the population (biomass) remaining after harvest.

The assumption here is that the relationship (1) holds exactly, but e_t is not observed directly. The connection between the observed effort and the effective effort is assumed to be given by

$$(2)\quad E_t = e_t \exp(v_t),$$

where the variables v_t are independent, normally distributed random variables with mean 0 and variance σ_v^2. We can assume that v_t has mean 0, since a non-zero mean can be absorbed into the parameter q.

Stock dynamics are assumed to be governed by the Ricker stock−recruitment relationship:

$$(3)\quad N_{t+1} = S_t \exp(\alpha - \beta S_t + u_t),$$

where

$$(4)\quad S_t = N_t - C_t = N_t \exp(-qe_t),$$

α and β are parameters, and u_t are independent, normally distributed random variables with mean 0 and variance σ_u^2.

Many fisheries scientists would argue that the Ricker model is inappropriate for most iteroporous fish stocks, and better results would be obtained from a more conventional surplus production model. We have chosen the Ricker model because it is explicitly a gross oversimplification of the stock dynamics, as all models, even age-structured models, must be gross oversimplifications of a vastly more complex real world. Hilborn (1979) showed that the traditional surplus production models fail to manage overexploited stocks, and he suggested that the reason was not their simplicity, but a lack of contrast in the data. We will show later in this paper that the simple structure of the Ricker model is not important; the problems are due to errors in estimates of abundance and lack of contrast, not simplicity.

Our objective is to estimate the parameters q, α, β, and σ_v^2,

in terms of observations C_t and E_t, for $t = 1, \ldots, T$. This cannot be done without an additional assumption, as is pointed out by Kendall and Stewart (1973). Here we imitate the procedure of Ludwig and Walters (1981), and we assume that

$$(5) \quad \sigma_v^2 = \lambda\sigma_u^2,$$

where the ratio λ is fixed beforehand. Of course, the choice of λ will affect the parameter estimates and the estimate of σ_v^2. For this reason, one ought to attempt to estimate σ_v^2 by means of a more elaborate data collection scheme. However, our main conclusions are qualitative rather than quantitative, and they are not sensitive to the choice of λ in the range $0.5 \leq \lambda \leq 1.5$. Our later numerical results were obtained with the choice $\lambda = 1$.

The basic variables N_t and S_t may be expressed in terms of e_t and the observed C_t as follows: from (1) and (2) we obtain

$$(6) \quad N_t = C_t/(1 - \exp(-qe_t)).$$

Then (4) yields S_t. The stock–recruitment relationship may be visualized by plotting $\ln(N_{t+1}/S_t)$ against S_t. In fact, (3) implies that

$$(7) \quad Y_t = \ln\frac{(N_{t+1})}{S_t} = \alpha - \beta S_t + u_t.$$

Thus α and β may be obtained from a linear regression, once values of q and $e_1, \ldots, e_T$ are assumed or estimated.

The details of the parameter estimation scheme are presented in Appendix A. The results are illustrated in Fig. 1. First measurement errors were neglected, i.e. we set $v_1 = 0, \ldots, v_T = 0$. The value of q was estimated by minimizing the sum of squares of the residuals in (7). The resulting values for $\ln(N_{t+1}/S_t)$ and S_t are plotted as numbers in Fig. 1. The dashed line is the corresponding regression line. Then, using the same value of q, the corrected efforts $e_1, \ldots, e_T$ were found by maximizing an appropriate likelihood of the observations. The parameter q was estimated before $e_1, \ldots, e_T$ in order to save computer time. The simulations described below suggest that this approximation is satisfactory. The result of "correcting" the observations is the set of open points, which are connected to the original points by line segments. The "corrected" regression line is shown as a solid line. The slope is less in magnitude than the slope of the uncorrected line. This phenomenon was observed for every set of data which we tried. Apparently, the observation errors introduce a bias in the estimation. Because of the complexity of the relations (1)–(4), we did not attempt to compute this bias, but simulation results are presented below.

Uncertainty In Parameter Estimates

The accuracy of the parameter estimates can be investigated by examination of the posterior parameter distribution, as in Ludwig and Walters (1981). Details are given in Appendix A. The result is illustrated in Fig. 2. There, a pair of 68% confidence intervals is drawn around the corrected regression line. The inner confidence interval represents uncertainty in the regression line itself, due to uncertainty in the parameters α and β. The outer confidence interval represents uncertainty in the complete stock–recruitment relationship, since it takes account of the variables u_t. Thus, one expects that 68% of the corrected data points will lie within the outer confidence interval.

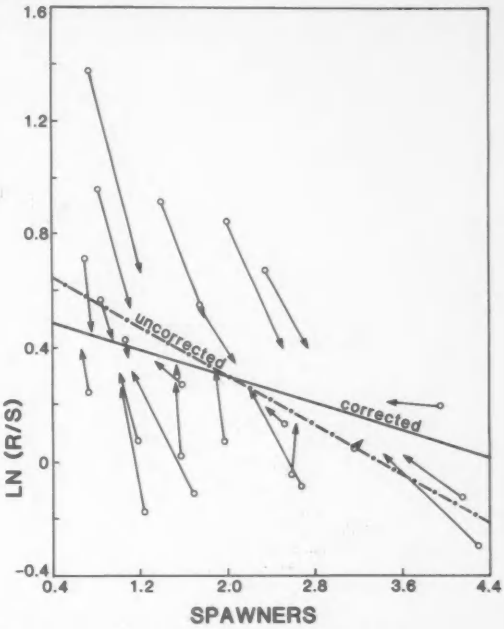

FIG. 1. Uncorrected and corrected data and regression lines, using a Ricker surplus production model. Data are for rock sole in Hecate Strait, B.C. for 1954–77. The uncorrected data points are shown as open circles. They are joined to the corrected points by arrows. The uncorrected regression line is dashed, while the corrected line is solid.

A similar procedure leads to coefficients of variation for α and β. These are obtained by dividing the standard deviation of the respective marginal posterior distribution by the mean of the posterior distribution. This measure of uncertainty appears to be appropriate for management strategies, in light of further calculations, using the method of Ludwig and Walters (1982). A similar coefficient of variation was computed for q, by consideration of the variation of the residual sum of squares in the regression (7), as a function q. Details are given in Appendix A.

To test the effectiveness of our estimation procedure, we generated 100 sets of simulated data for 25 yr of catches and efforts from our model (1)–(5), using $\alpha = 0.5$, $\beta = 1$, $q = 1$, $\sigma_u = 0.3$, $\lambda = 1$. A sequence of efforts with $E_{max}/E_{min} = 4$ were chosen. This resulted in moderate contrast in the data. Then the parameters α, β, and q were estimated without correcting for observation errors, i.e. by setting $e_t = E_t$, $t = 1, \ldots, T$. The "optimal" effort E^* was then estimated by maximizing yield at equilibrium, using the Ricker model. The resulting biases and coefficients of

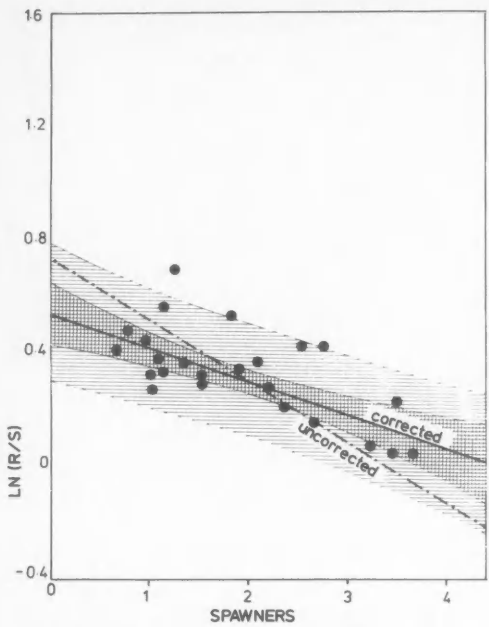

FIG. 2. Confidence regions for the corrected regression which is shown in Fig. 1. The inner shaded region has a width of one standard error in the regression variable on either side. The outer shaded region has a width of one standard error for the data points on either side.

variation are displayed in Table 1, under the columns labeled "uncorrected." The corresponding quantities were also computed using the procedure of Appendix A with $\lambda = 1$. These are labeled "corrected." The most striking changes occur in the estimates for β. The bias is reduced by a factor of 6.5, and the coefficient of variation is increased by a factor of 10. This produces two beneficial effects: spurious density dependence is reduced, and the reliability of the estimate of β is decreased. Since the observation errors do in fact reduce the reliability of this estimate, the corrected results are more appropriate. Further simulations show that the effect of observation errors decreases sharply as contrast in the data increases. In particular, the correction procedure makes only slight improvement if $E_{max}/E_{min} = 8$.

A Probing Strategy

It is not possible to compute an optimal harvesting strategy for the present problem, because of the "curse of dimensionality." The true optimal strategy depends upon the estimated stock size $\hat{N}_T$, the parameter estimates $\hat{\alpha}$, $\hat{\beta}$, and $\hat{q}$, and their covariance matrix. Thus, it is a function of 9 variables. Its computation would involve the true values of α, β, and q as well. Thus, a dynamic programming approach would involve solution of a problem with a total of 12 independent variables. Such a computation is far beyond reach of any computer.

TABLE 1. Results of 100 Monte Carlo simulations of the estimation procedure, with and without our correction for the effective effort. The coefficients of variation are averages of those estimated from the data, at each trial.

	Bias		Coefficient of Variation	
Parameter	Uncorrected	Corrected	Uncorrected	Corrected
α	0.106	0.060	0.24	0.20
β	1.04	0.160	0.64	6.4
q	0.19	0.16	0.25	0.17
E^*	0.054	−0.0066	—	—

Nevertheless, one can attempt to find a reasonable strategy, by analogy with the simple case of a single unknown parameter, as described in Ludwig and Walters (1982). Those computations showed that the optimal escapement is nearly independent of the coefficient of variation of the unknown parameter, if that coefficient is less than 0.5. As the coefficient increases beyond 0.5, the optimal escapement increases abruptly, by a factor of 2. For very slowly growing stocks, the optimal escapement decreases by a factor of 2. Thus, apparently one may ignore parameter uncertainty until a threshold is reached. Beyond the threshold, one should probe strongly, in order to gain information as quickly as possible.

How should the effort be manipulated in order to gain the most information? A complete solution of this problem is impossible, for the reasons stated above. However, Hilborn (1979) offers some heuristic principles. To estimate the parameters, sufficient contrast is required in both the effort and the catch per unit effort. Roughly speaking, contrast in effort is necessary to estimate the catchability, and contrast in catch per unit effort is necessary to estimate α and β. Here "contrast" means variation by at least a factor of 3.

For the present problem, these ideas suggest that a decision to probe should be based upon examination of the coefficients of variation of α, β, and q. If any of the latter exceeds its respective tolerance, probing should take place. Otherwise, deterministic theory may be used to determine the effort. If the decision to probe has been made, should the effort be increased or decreased? The answer depends upon which parameter most exceeds its tolerance. If q is the worst offender, we have chosen to make the effort as large as possible. The reason is that q only appears when multiplied by E, and thus q cannot be estimated unless there are large contrasts in the values of E. If the greatest uncertainty lies in the stock–recruitment parameters α and β, low values of E are assigned. The idea is to generate contrast in catch per unit effort by allowing the stock to recover from harvesting pressure.

The strategy which was used in the simulations is summarized in Fig. 3. The tolerances for the coefficient of variation of α, β, and q were determined by trial and error, using the simulation described below. Values which worked well were 0.75, 0.75, and 1.75, respectively. If less than 20 yr of data were available, these tolerances were divided by 2. This has the effect of encouraging probing in the early years, when there is a danger of being misled by data from overexploited stocks. This phenomenon is described in more detail below.

The preceding strategy worked well for the simulations described below. It was chosen with programming con-

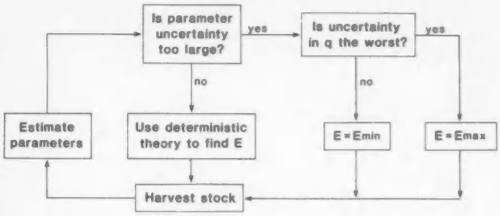

FIG. 3. Flow chart for the probing strategy which was employed for the simulations.

venience in mind. We do not recommend that it be followed slavishly, but that efforts be manipulated to produce the required contrast in both effort and catch per unit effort. Our experience with simulations suggests that α and β (especially β) can be estimated accurately only if the stock size varies by approximately a factor of 4. Likewise, q will be estimated most quickly if E varies abruptly and strongly. This is an important difference from "optimal" strategies which assume perfect information. With perfect information, a stabilization of biomass policy will maximize the sustained yield, or a discounted total yield over time. We suggest that a strategy of pulse harvesting is superior, if there is substantial uncertainty about the parameter values.

Simulation Results

The strategy described above was developed and tested with the simulation model of Hilborn (1979). The most awkward case is that of a slowly growing, severely overexploited stock (model A "overexploited" in the terminology of Hilborn). Hilborn tested five harvesting strategies, and all of them held the stock down at the overexploited level. An occasional exception was Schnute's estimation scheme, which sometimes performed reasonably well. But its performance was erratic; often negative parameter estimates were obtained.

The cause of the failures is apparently a spurious density dependent effect in recruitment, which is caused in part by errors in the measurement of the effective effort in analogy with Walters and Ludwig (1981). A possible additional bias is due to the simplistic stock–recruitment relationships which were employed. However, a similar effect is observed when employing the estimation scheme of Deriso (1980) (C. Walters, Institute of Animal Resource Ecology, U.B.C., personal communication).

Although the causes of the bias are obscure, the effect is quite significant. In every case, regardless of the estimation scheme which was employed, the initial estimate of the optimal biomass was far too low, by a factor of 5 to 10. The error correction scheme described in Appendix A generally corrected some of the bias. The uncorrected, corrected, and "exact" relationship are shown in Fig. 4. The "exact" relationship was obtained by requiring that the Ricker model lead to the correct biomass and effort at the optimal equilibrium state.

The error correction scheme by itself was not able to improve overall performance of the strategy, since it still tended

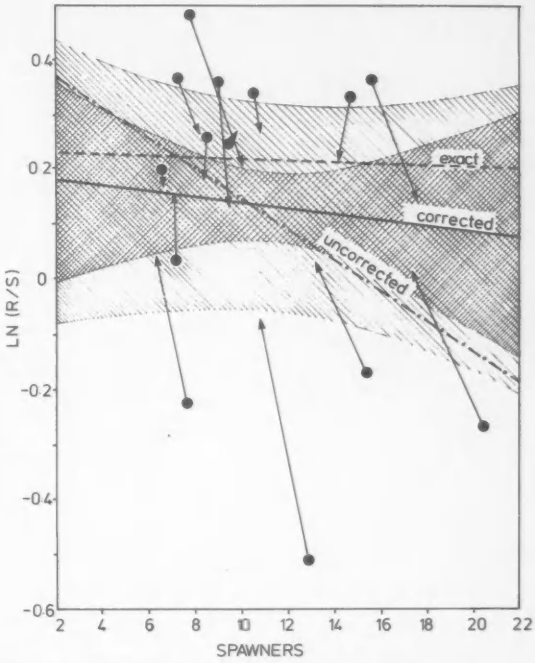

FIG. 4. Uncorrected and corrected data and confidence regions for some simulated data. Since the exact parameter values are known, the exact regression line is also displayed.

to get stuck in the overexploited state. We found it necessary to do two additional things: (1) discount past data (5% per year worked well), (2) utilize a probing strategy, as described in the previous section. The combination of error correction and discounting greatly increased the estimate of parameter uncertainty, to a point where probing was indicated. Once probing had begun, and the stock had shown signs of recovery, the accuracy of parameter estimates improved. However, reliable and accurate estimates appeared only after the stock had exceeded MSY level, and perhaps oscillated around it for some time.

Our probing strategy was further tested against the "unexploited" and "equilibrium" cases of Model A of Hilborn (1979), in order to assess its robustness. Performance was better than any of the nonprobing strategies of Hilborn, and was nearly as good as constant effort strategy with perfect information. The results are shown in Table 2.

A Revised Probing Strategy

Although the performance of the probing strategy is generally good, there is room for improvement. We were able to make a considerable improvement by analyzing the reasons for the lowest percentage yields in Table 2. In most cases, the low yields were caused by very heavy exploitation in the first few years of management. The heavy exploitation was, in

TABLE 2. Total yield from a 50-yr simulation, expressed as a percentage of the yield obtainable with perfect information. A probing strategy was employed for these kinds of starting conditions.

Seed	Overexploited	Equilibrium	Unexploited
1.104	85%	91%	94%
2.104	77	92	89
3.104	76	89	89
4.104	66	94	87
5.104	75	89	71
6.104	76	89	77
7.104	90	96	82
8.104	80	—	—
9.104	79	—	—
Average	78%	91%	84%

turn, a consequence of poor estimates of the parameter q.

This defect in the strategy was removed by revising the procedure during the first 10 yr of management. Hilborn's simulation procedure initially generates 5 yr of rather uninformative data. The revised strategy then chooses a very low effort for the next 5 yr to determine whether or not the stock was overexploited. This was tested by comparing the average catch per unit of effort for the first 5-yr period with the corresponding quantity for the next 5-yr period. If the ratio of these two quantities was less than 0.8, efforts were held at a minimal level for an additional 5-yr period. At the end of that period, the earlier probing strategy was followed. If the ratio of averaged catch per unit effort was greater than 0.8, a maximal effort was chosen for the next 2 yr.

This revised strategy worked surprisingly well. The simple test of the ratio of averaged catch per unit effort distinguished the unexploited stock from the equilibrium stock and the overexploited stock in every case. The effect of the 10-yr waiting period was to provide good evidence of recovery of the stock. The earlier probing strategy then was able to manage the stock in a near-optimal manner. The 5 yr of low harvest made very little difference to the total yield, when the stock was initially unexploited. The results are displayed in Table 3.

Conclusion

The simulation results demonstrate that it is possible to manage stocks to obtain near-optimum yields, when an index of abundance such as CPUE is available. In particular, the effects of errors in observations can be overcome by means of a sophisticated estimation scheme, provided that sufficient contrast is present in the data. Likewise, the Ricker model was found to be an adequate basis for management, even for a stock with age structure. Thus, we argue that the reason fisheries stock assessment methods fail to produce good estimates of productive potential is not simplicity of the model as is often argued, but poor contrast in the data.

There are two important qualifications to these conclusions: (1) the performance was evaluated without discounting future returns, and (2) the economic and social effects of sharp and irregular changes in effort were ignored. These qualifications raise serious questions about the applicability of this work, which we address below.

TABLE 3. Total yield for a 50-yr simulation, expressed as a percentage of the yield obtainable with perfect information. The revised probing strategy was employed.

Seed	Overexploited	Equilibrium	Unexploited
1.104	100%	97%	95%
2.104	90	88	89
3.104	86	94	87
4.104	84	91	88
5.104	95	90	96
Average	91%	92%	91%

Discussion

The algorithm developed in the main part of this paper suggests rules for deciding when to shut down a fishery for an experimental period. If we accept that it may take a long time to detect the recovery of a stock, are such experimental closures practical? Perhaps not. To our knowledge no fishery has ever been closed for conservation unless there was very strong evidence that it was overexploited, or there were substantial alternative fishing opportunities elsewhere. The examples of the B.C. herring, Bristol Bay sockeye, Pacific halibut, and North Pacific fur seal mentioned in the introduction each involved cases where there was strong evidence for overexploitation. Fisheries managers and fishermen may be unwilling to drastically reduce a fishery on an experimental basis, unless there are other fishing opportunities. However, the system of area licensing permits provides a flexible tool for such experimental closures.

In many cases, there are alternative fishing opportunities, and experimental closures can be implemented because they do not impose undue hardships on fishermen. The closure of Rivers Inlet in B.C. to sockeye salmon fishing in 1980 is an example of such an experiment. The best scientific evidence indicates that the stock is overexploited, but the evidence is not unequivocal. Without the alternative fishing opportunities we suspect the current closure would not have been implemented. Most recently, Tyler et al. (1981) have proposed an experimental fishing plan for the Oregon trawl fisheries that sets aside specific trawling grounds for experimental periods of lower fishing efforts, again relying on alternative fishing grounds to support the fishermen during the experimental period. Tyler et al.'s proposals have the essential ingredients for a generalized experimental fishing plan which could take place even with a single stock.

We propose that experimental management plans be formulated which identify space time areas of a fishery that may be treated as semi-isolated studies. An example might be two trawling grounds with the same species of fish, which show similar abundance and have a similar exploitation history. If the costs of fishing the two grounds are similar, we would expect the fishery to have maintained the abundance at similar levels. An experimental fishing plan would deliberately distort the fishing effort on these two grounds, placing perhaps 90% of the effort on one ground and only 10% on the other. If the stocks were overexploited, we would expect to see recovery of the stock on the ground receiving only 10% of the effort. Once this recovery was observed, and could be differ-

entiated from the increase in abundance we would expect from any stock with a reduction in fishing effort, then the uncertainty would be reduced and an overall reduction in fishing effort on both grounds implemented. If the stocks on these two grounds were not overexploited, then we would fail to see dramatic recovery on the less exploited ground, and we could revert to the previous fishing policies. The market forces should direct more effort to the ground receiving 10% of effort during the experimental phase, since the abundance at the end of the experiment should be higher on this ground.

Such two-area experimental fishing plans are subject to at least one major problem: the dynamics of the two areas must be largely independent. If we are attempting to detect the recovery of a potentially overexploited stock after reducing fishing effort, then immigration must not constitute a significant portion of the recruitment. The ideal type of stock for such an experiment would be one that had little larval or juvenile mixing of stocks. Species with wide ranging larval movements such as Pacific halibut would be unsuited for such experiments. A species with a history of tagging studies establishing movement patterns would be a likely candidate.

Now we turn to the question of whether future returns should be discounted, when harvesting strategies are evaluated. From an economic standpoint, such discounting would appear to be mandatory; the discount rate should be comparable to the opportunity cost of capital (Clark 1976, p. 72). Clark also shows that if the discount rate exceeds the net reproductive rate of the population, the optimal harvest policy may be to harvest the population to extinction. But these conclusions are based upon the assumption that the goal of management is to maximize profit, or perhaps some more general social utility. On the other hand, fisheries are generally regulated by governmental agencies or international commissions. Their mandate is often stated vaguely, but generally will include some phrase such as "best use of the resource," or perhaps even refer to a "maximum sustainable yield." In either case, extinction of the resource is hardly compatible with such a mandate.

The present case is less extreme, but the same principle is at stake. Is it compatible with the mandated goals of management to allow a stock to remain in an overexploited condition, or to ignore the possibility that the stock may be overexploited? How high a price should we pay in pursuit of a goal of steady yields?

Since we argued earlier that our proposed policy of experimental management provides near optimal yield from potentially overexploited stocks, and we also stated that these policies are not practical, we must believe that most fisheries managers and fishermen are not attempting to maximize long term yield. The managers' objectives may differ from MSY in many ways: they may have a high discount rate on future returns, they may have strong risk aversion to possible closures without increased returns, or they may simply value stability of yield greater than average yield. Each of these is a legitimate real world objective, but it is not often recognized how different the policy consequences are for each of these objectives.

If experimental closures are not practical, then some explicit examination and statement of the management objectives seems to be in order.

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Appendix A

Estimation of Parameters and Observation Errors

This appendix provides details of the scheme for estimating the parameters q, α, and β, and for obtaining the effective efforts $e_1, \ldots, e_T$. The procedure is similar to that employed in Ludwig and Walters (1981). The parameters are estimated by maximizing an appropriate likelihood of the observations. Uncertainty in our knowledge of the parameters is estimated by considering the posterior density for the parameters, assuming a flat prior distribution. Observations may be weighted according to their presumed reliability. Prior information may be included by assigning low weights to less reliable observations.

The Likelihood Function

The data consist of observations of catch C_t and effort E_t for $t = 1, \ldots, T$. The stock size before harvest in year t is given by (6). Then the biomass of spawners after harvest is given by (4). In view of (7), the residuals in the stock–recruitment relationship are given by

$$u_t = y_t - \alpha + \beta S_t. \tag{A.1}$$

Note that u_t depends upon q and $e_1, \ldots, e_T$, as well as α and β. The likelihood of the observations is given by an integral over $e_1, \ldots, e_T$ of

$$L = \exp\Big[- \frac{M(\alpha, \beta, q, e)}{\sigma_u^2} - \sum_{t=1}^{T-1} w_t \ln \sigma_u - \sum_{t=1}^{T} w_t \ln \hat{\sigma}_v \Big], \tag{A.2}$$

where

$$M(\alpha, \beta, q, e) = \frac{1}{2} \sum_{t=1}^{T-1} w_t u_t^2 + \frac{1}{2\lambda} \sum_{t=1}^{T} w_t v_t^2, \tag{A.3}$$

and $w_1, \ldots, w_T$ are weights which are assigned to the respective observations. Note that (5) has been employed to eliminate σ_v^2 in (A.3). The true likelihood, which is the integral of L, will be approximated by a multiple of its maximum value with respect to $e_1, \ldots, e_T$. This approximation is expected to be accurate, since L is approximately a Gaussian density with respect to $\ln e_1, \ldots, \ln e_T$. Thus the variables $e_1, \ldots, e_T$ may be dealt with as if they were nuisance parameters to be estimated.

Maximizing the Likelihood

The likelihood will be maximized if M is minimized as a function of all its arguments. To simplify the computations, the parameter q is treated separately. The following procedure will be carried out for a fixed value of q, because of its similarity to an ordinary linear regression. Finally, q will be determined by minimizing the resulting sum of squares of residuals.

The parameters α, β, and $e_1, \ldots, e_T$ may be determined by setting the corresponding partial derivatives of M equal to zero. In view of (2), we may regard $e_1, \ldots, e_T$ as functions of $v_1, \ldots, v_T$, and calculate as if $v_1, \ldots, v_T$ are parameters to be estimated. Thus, at the minimizing values $\hat{\alpha}, \hat{\beta}, \hat{v}$ we must have

$$\frac{\partial M}{\partial v_r}(\hat{\alpha}, \hat{\beta}, q, \hat{v}) = \sum_{t=1}^{T-1} w_t \hat{u}_t \frac{\partial \hat{u}_t}{\partial v_r} + \frac{1}{\lambda} w_r \hat{v}_r = 0, \quad r = 1, \ldots, T, \tag{A.4}$$

$$-\frac{\partial M}{\partial \alpha}(\hat{\alpha}, \hat{\beta}, q, \hat{v}) = \sum_{t=1}^{T-1} w_t \hat{u}_t = 0. \tag{A.5}$$

$$\frac{\partial M}{\partial \beta}(\hat{\alpha}, \hat{\beta}, q, \hat{v}) = \sum_{t=1}^{T-1} w_t \hat{u}_t \hat{S}_t = 0. \tag{A.6}$$

Note that (A.5) and (A.6) are just the equations for a linear regression, once the corrected efforts $e_1, \ldots, e_T$ have been found.

Newton's Method

Since the system (A.4) is nonlinear in v, we shall solve it by an iterative method. A first approximation is obtained by setting $v_t = 0$ for $t = 1, \ldots, T$, and solving the linear system (A.5), (A.6) for α and β. The resulting approximation will be denoted by v_t^o, α^o, β^o. We attempt to represent the true solution in the form

$$\alpha = \alpha^o + \delta\alpha, \ \beta = \beta^o + \delta\beta, \ v_t = v_t^o + \delta v_t. \tag{A.7}$$

These expressions may be inserted into (A.4). Then (A.4) may be expanded by Taylor's theorem. If quadratic and higher powers of $\delta\alpha$, $\delta\beta$, and δv_t are neglected, the result is the approximating linear system

$$\frac{\partial M}{\partial v_r} + \sum_{s=1}^{T} \frac{\partial^2 M}{\partial v_r \partial v_s} \partial v_s + \frac{\partial^2 M}{\partial v_r \partial \alpha} \delta\alpha + \frac{\partial^2 M}{\partial v_r \partial \beta} \delta\beta = 0, \ r = 1, \ldots, T. \tag{A.8}$$

In (A.8)–(A.14) the derivatives of M are evaluated at $(\alpha^o, \beta^o, q, v^o)$. These coefficients are evaluated in Appendix B.

The system (A.8) may be regarded as a system of linear equations for $\delta v_1, \ldots, \delta v_T$; the solution depends upon the additional variables $\delta\alpha$ and $\delta\beta$. In fact, the solution of (A.8) is a combination of the solutions of three systems of linear equations, which differ only in their inhomogeneous terms. Thus, we let $g_1, \ldots, g_T$ be the solution of

$$\sum_{s=1}^{T} \frac{\partial^2 M}{\partial v_r \partial v_s} g_s = \frac{\partial M}{\partial v_r}, \ r = 1, \ldots, T, \tag{A.9}$$

and we let $h_{\alpha s}$ and $h_{\beta s}$ be the solutions of

$$\sum_{s=1}^{T} \frac{\partial^2 M}{\partial v_r \partial v_s} h_{\alpha s} = \frac{\partial^2 M}{\partial v_r \partial \alpha}, \ r = 1, \ldots, T, \tag{A.10}$$

$$\sum_{s=1}^{T} \frac{\partial^2 M}{\partial v_r \partial v_s} h_{\beta s} = \frac{\partial^2 M}{\partial v_r \partial \beta}, \ r = 1, \ldots, T. \tag{A.11}$$

Then the solution of (A.8) is given by

$$\delta v_r = -g_r - h_{\alpha r} \delta\alpha - h_{\beta r} \delta\beta, \ r = 1, \ldots, T. \tag{A.12}$$

Now a similar procedure may be applied to (A.5) and (A.6). The linear approximating equations are

$$\frac{\partial M}{\partial \alpha} + \frac{\partial^2 M}{\partial \alpha \partial v_r} \delta v_r + \frac{\partial^2 M}{\partial \alpha^2} \delta\alpha + \frac{\partial^2 M}{\partial \alpha \partial \beta} \delta\beta = 0, \tag{A.13}$$

and the same equation with α and β interchanged. Now (A.12) may be substituted into (A.13). The result is

$$\text{(A.14)}\quad \frac{\partial M}{\partial \alpha} - \sum_{r=1}^{T} \frac{\partial^2 M}{\partial \alpha \partial v_r} g_r + \left(\frac{\partial^2 M}{\partial \alpha^2} - \sum_{r=1}^{T} \frac{\partial^2 M}{\partial \alpha \partial v_r} h_{\alpha r} \right) \delta\alpha + \left(\frac{\partial^2 M}{\partial \alpha \partial \beta} - \sum_{r=1}^{T} \frac{\partial^2 M}{\partial \alpha \partial v_r} h_{\beta r} \right) \delta\beta = 0,$$

and the same equation with α and β interchanged. This pair of equations may be solved for $\delta\alpha$ and $\delta\beta$. The resulting values may be substituted into (A.12). Finally, (A.7) may be used to update the values of α, β, and v_t.

In general, a single iteration of this kind will not satisfy (A.4)−(A.6) to sufficient accuracy. The procedure may then be repeated, replacing α^o, β^o, and v^o by the latest approximation. Convergence of these iterations can be assured if the parameter λ is suitably manipulated, and the estimates are extrapolated in λ. Details of this process are given in Ludwig and Walters (1981). They will not be repeated here.

Uncertainty in the Parameter Estimates

The posterior parameter distribution involves $e_1, \ldots, e_T$ as well as α and β. Since our primary concern is with α and β, we eliminate $e_1, \ldots, e_T$ by solving (A.4) for $v_1, \ldots, v_T$;

$$\text{(A.15)}\quad \frac{\partial M}{\partial v_r}(\alpha, \beta, q, V(\alpha, \beta)) = 0,\ r = 1, \ldots, T.$$

The derivatives of V with respect to α and β may be computed by differentiating (A.15):

$$\text{(A.16)}\quad \frac{\partial^2 M}{\partial v_r \partial \alpha} + \sum_{s=1}^{T} \frac{\partial^2 M}{\partial v_r \partial v_s} \frac{\partial V_s}{\partial \alpha} = 0,\ r = 1, \ldots, T.$$

A similar equation results if α is replaced by β. If these equations are compared with (A.10) and (A.11), it is clear that

$$\text{(A.17)}\quad h_{\alpha s} = -\frac{\partial V_s}{\partial \alpha},\ h_{\beta s} = -\frac{\partial V_s}{\partial \beta},\ s = 1, \ldots, T.$$

At the point $\hat{\alpha}, \hat{\beta}, V(\hat{\alpha}, \hat{\beta})$ where (A.5) and (A.6) are satisfied, the total second derivatives of M are given by

$$\text{(A.18)}\quad M'_{\alpha\alpha} = \frac{\partial^2}{\partial \alpha^2} M(\alpha, \beta, q, V(\alpha, \beta)) = \frac{\partial^2 M}{\partial \alpha^2} + \sum_{r=1}^{T} \frac{\partial^2 M}{\partial \alpha \partial v_r} \frac{\partial V_r}{\partial \alpha} = \frac{\partial^2 M}{\partial \alpha^2} - \sum_{r=1}^{T} \frac{\partial^2 M}{\partial \alpha \partial v_r} h_{\alpha s},$$

$$\text{(A.19)}\quad M'_{\alpha\beta} = \frac{\partial^2}{\partial \alpha \partial \beta} M(\alpha, \beta, q, V(\alpha, \beta)) = \frac{\partial^2 M}{\partial \alpha \partial \beta} - \sum_{r=1}^{T} \frac{\partial^2 M}{\partial \beta \partial v_r} h_{\beta r}$$

$$\text{(A.20)}\quad M'_{\beta\beta} = \frac{\partial^2}{\partial \beta^2} M(\alpha, \beta, q, V(\alpha, \beta)) = \frac{\partial^2 M}{\partial \beta^2} - \sum_{r=1}^{T} \frac{\partial^2 M}{\partial \beta \partial v_r} h_{\beta r}.$$

These derivatives are the coefficients which appear in (A.14) and its relative with α and β interchanged. The coefficients may be interpreted as elements of a reduced information matrix, which takes account of the effect of the observation errors.

If (A.4)−(A.6) are satisfied at $\hat{\alpha}, \hat{\beta}, V(\hat{\alpha}, \hat{\beta})$, we may approximate M by

$$\text{(A.21)}\quad M(\alpha, \beta, q, V(\alpha, \beta)) \sim M(\hat{\alpha}, \hat{\beta}, q, V(\hat{\alpha}, \hat{\beta})) + \frac{1}{2}[M'_{\alpha\alpha}(\alpha - \hat{\alpha})^2 + 2M'_{\alpha\beta}(\alpha - \hat{\alpha})(\beta - \hat{\beta}) + M'_{\beta\beta}(\beta - \hat{\beta})^2]$$

In view of (A.21), the posterior distribution for α and β is approximated by a bivariate normal distribution. The variance of this distribution is determined by the value of σ_u^2. An unbiased estimate for σ_u^2 is

$$\text{(A.22)}\quad \hat{\sigma}_u^2 = \frac{1}{T-3}\left[\sum_{t=1}^{T-1} w_t \hat{u}_t^2 + \frac{1}{\lambda} \sum_{t=1}^{T} w_t \hat{v}_t^2 \right]$$

The formula (A.22) is a departure from a strict Bayesian approach to the estimation problem, since σ_u^2 will actually have a Gamma distribution. The simpler form (A.22) seems to be adequate for our purposes.

The confidence intervals in Fig. 2, and the coefficients of variation for α and β are obtained from (A.2), (A.21) and (A.22).

Estimation of q

The preceding analysis has required that q be fixed. As q varies, $\hat{\alpha}$, $\hat{\beta}$, and $\hat{\sigma}_u^2$ will also vary. Hence the likelihood given by (A.2) is a function of q. If $\alpha = \hat{\alpha}$, $\beta = \hat{\beta}$, and $\sigma_u^2 = \hat{\sigma}_u^2$, then substitution of (A.22) into (A.2) yields

$$\text{(A.23)}\quad L = \exp[-(T-3) - \left(\sum_{t=1}^{T-1} w_t\right) \ln \hat{\sigma}_u - \left(\sum_{t=1}^{T} w_t\right)(\ln \sqrt{\lambda} + \ln \hat{\sigma}_u)].$$

If factors which are independent of q are neglected, we obtain

$$\text{(A.24)}\quad L \sim \exp[-W \ln \hat{\sigma}_u],$$

where

$$\text{(A.25)}\quad W = \sum_{t+1}^{T} w_t + \sum_{t+1}^{T} w_t$$

The maximum likelihood estimate of q will be that value $\hat{q}$ which minimizes $\hat{\sigma}_u$; thus the sum of squares of residuals in (A.22) is a minimum at $\hat{q}$. This is a relatively simple minimization problem, since it involves a search over a single parameter. Many methods are available for such problems. The present calculations were performed by a method which combines subdivision and quasi-Newton steps. The output is a set of three values of q: q_1, q_2, and q_3, where $\hat{\sigma}_u(q)$ has a minimum near q_2, lying between q_1 and q_3.

In the vicinity of these three points, $\ln \hat{\sigma}_u(q)$ may be

represented by an interpolating polynomial of degree 2 in $\ln q$, with a minimum at $\ln \hat{q}$. The result is a representation.

$$(A.26)\quad L \sim \exp[-W(\ln \hat{\sigma}_u(q)) + \frac{W}{2} A(\ln q - \ln \hat{q})^2].$$

Here A is the second derivative of the interpolating polynomial at $\ln q = \ln \hat{q}$. Thus the posterior density for $\ln q$ is approximately normal, with mean $\ln \hat{q}$, and variance V_q^2, where

$$(A.27)\quad V_q = \frac{1}{\sqrt{WA}}$$

The quantity V_q is our estimated coefficient of variation of q.

Appendix B

Calculation of Some Coefficients

Equations (A.4) and (A.8)–(A.11) have coefficients which involve first and second derivatives of M. As we shall see, these coefficients may be calculated in terms of first and second derivatives of u_t with respect to v.

First Derivatives of u_t

The following calculations are simplified if we introduce

$$(B.1)\quad p_t = 1 - \exp(-qe_t),$$

where

$$(B.2)\quad e_t = E_t \exp(-v_t).$$

Then (6) takes the form

$$(B.3)\quad N_t = C_t/P_t,$$

and

$$(B.4)\quad S_t = C_t\left(\frac{1}{p_t} - 1\right).$$

Now we set

$$(B.5)\quad p_t' = \frac{\partial p_t}{\partial v_t} = -qe_t \exp(-qe_t),$$

and similarly

$$(B.6)\quad p_t'' = \frac{\partial^2 p_t}{\partial^2 v_t} = (qe_t - 1)p_t'.$$

From (7), (B.3) and (B.4), it follows that

$$(B.7)\quad u_t = \ln\left(\frac{C_{t+1}}{p_{t+1}}\right) - \ln\left(C_t\left(\frac{1}{p_t} - 1\right)\right) - \alpha + \beta C_t\left(\frac{1}{p_t} - 1\right).$$

Note that p_t depends upon v_t, but is independent of v_s if $s \neq t$. Thus we have

$$(B.8)\quad \frac{\partial u_t}{\partial v_{t+1}} = -\frac{p'_{t+1}}{p_{t+1}},$$

and

$$(B.9)\quad \frac{\partial u_t}{\partial v_t} = \frac{p'_t}{p_t^2}\left[\frac{p_t}{1-p_t} - \beta C_t\right]$$

The derivatives of u_t with respect to v_s are zero if $s \neq t$ and $s \neq t+1$. If (B.8) and (B.9) are inserted into (A.4), the result is

$$(B.10)\quad \frac{\partial M}{\partial v_r} = w_r u_r \frac{p'_r}{p_r^2}\left[\frac{p_r}{1-p_r} - \beta C_r\right] + w_{r-1} u_{r-1}\left(\frac{-p'_r}{p_r}\right) + \frac{1}{\lambda} w_r v_r,\ r = 1, \ldots, T.$$

This formula is required for (A.8) and (A.9). If (B.10) is differentiated with respect to α and β, the result is

$$(B.11)\quad \frac{\partial^2 M}{\partial v_r\, \partial \alpha} = -w_r \frac{p'_r}{p_r^2}\left[\frac{p_r}{1-p_r} - \beta C_r\right] + w_{r-1}\frac{p'_r}{p_r},$$

and

$$(B.12)\quad \frac{\partial^2 M}{\partial v_r\, \partial \beta} = w_r S_r \frac{p'_r}{p_r^2}\left[\frac{p_r}{1-p_r} - \beta C_r\right] - w_{r-1} S_{r-1}\frac{p'_r}{p_r} - w_r u_r \frac{p'_r}{p_r} C_r.$$

Second Derivatives of u_t

To compute the remaining coefficients in (A.10) and (A.11), we shall require second derivatives of u_t with respect to v. From (B.8) it is evident that $\dfrac{\partial u_t}{\partial v_{t+1}}$ depends only upon v_{t+1}. Thus

$$(B.13)\quad \frac{\partial^2 u_t}{\partial v_{t+1}^2} = \frac{-p''_{t+1}}{p_{t+1}} + \frac{(p'_{t+1})^2}{p_{t+1}^2}$$

Similarly, (B.9) implies that

$$(B.14)\quad \frac{\partial^2 u_t}{\partial v_t^2} = \frac{p''_t\, p_t - 2(p'_t)^2}{p_t^3}\left[\frac{p_t}{1-p_t} - \beta C_t\right] + \frac{p'_t}{p_t^2}\frac{p'_t}{(1-p_t)^2}$$

All of the other second derivatives of u_t with respect to v are zero.

Second Derivatives of M

It follows from differentiating (A.4) that

$$\text{(B.15)}\quad \frac{\partial^2 M}{\partial v_r^2} = w_r\left(\frac{\partial u_r}{\partial v_r}\right)^2 + w_r u_r \frac{\partial^2 u_r}{\partial v_r^2} + w_{r-1}\left(\frac{\partial u_{r-1}}{\partial v_r}\right)^2 + w_{r-1}u_{r-1}\frac{\partial^2 u_{r-1}}{\partial v_r^2}.$$

Similarly,

$$\text{(B.16)}\quad \frac{\partial^2 M}{\partial v_r\,\partial v_{r+1}} = w_r \frac{\partial u_r}{\partial v_{r+1}}\frac{\partial u_r}{\partial v_r} + w_r u_r \frac{\partial^2 u_r}{\partial v_r\,\partial v_{r+1}}.$$

The other second derivatives of M with respect to v are all zero. The forms (B.15) and (B.16) may be evaluated by substituting (B.8), (B.9), (B.13), and (B.14). Note that the last term in (B.16) vanishes, in view of the remark following (B.14). The coefficients given by (B.15) and (B.16) are then inserted into (A.19)–(A.11).

Anthropogenic Zinc and Cadmium Burdens in Sediments of Selected Southern Ontario Lakes

HAYLA E. EVANS

Freshwater Science Program, Trent University, Peterborough, Ont. K9J 7B8

P. JANE SMITH[1] AND PETER J. DILLON[1]

Ontario Ministry of the Environment, Box 213, Rexdale, Ont. M9W 5L1

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The concentrations of Cd and Zn were measured in the sediments of 10 softwater lakes in southern Ontario. Elevated Cd and Zn levels were present in the recently deposited sediments of all the lakes, despite the absence of local point-source inputs. Whole-lake anthropogenic Zn and Cd burdens, calculated by prorating site-specific burdens according to the ratio of the site-specific Pb burden to the whole-lake Pb burden, range between 322 and 617 $mg \cdot m^{-2}$ for Zn and between 6.2 and 11.3 $mg \cdot m^{-2}$ for Cd. There were no significant differences in anthropogenic Zn or Cd burdens between lakes. The lack of a relationship between Zn or Cd burdens and the ratio of watershed area to lake area or the water replenishment time of the lakes indicates that deposition from the atmosphere directly onto the lakes' surfaces is an important input of these metals to the lakes.

EVANS, H. E., P. J. SMITH, AND P. J. DILLON. 1983. Anthropogenic zinc and cadmium burdens in sediments of selected southern Ontario lakes. Can. J. Fish. Aquat. Sci. 40: 570 – 579.

Les concentrations de Cd et Zn ont été mesurées dans les sédiments de 10 lacs d'eau douce du sud de l'Ontario. Les niveaux de ces deux métaux sont élevés dans les sédiments nouvellement déposés de tous les lacs, en dépit de l'absence de sources ponctuelles locales. Les charges de Zn et Cd anthropogènes du lac entier, calculées en établissant la proportion entre les charges spécifiques au site et le rapport de la charge de Pb spécifique au site et celle de Pb du lac entier, sont comprises entre 322 et 617 $mg \cdot m^{-2}$ pour le Zn et 6,2 et 11,3 $mg \cdot m^{-2}$ pour le Cd. Il n'y a pas de différences significatives de charge de Zn ou Cd anthropogène d'un lac à l'autre. L'absence de relation entre les charges des deux métaux et le rapport superficie du bassin hydrographique/superficie du lac ou le temps de renouvellement de l'eau de lac indiquent qu'une déposition directe de ces métaux de l'atmosphère dans les eaux de surface est une source importante.

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IT has been well-documented that man's activities have altered the natural geochemical cycles of many trace metals including Zn and Cd. Localized contamination of terrestrial and aquatic environments with these two metals has been reported near mining and smelting operations (Gale et al. 1976; Ward et al. 1976; Semkin and Kramer 1976; Jeffries and Snyder 1981), near wastewater effluents (Wentsel and Berry 1974; Oliver and Agemian 1974; Wisseman and Cook 1977), and as a result of the use of certain biocides (Norton et al. 1978). Nonlocalized contamination, i.e. that not attributable to a nearby point source, although more poorly understood, is receiving increased attention.

The long-range transport of trace metals has been linked to the transport of other substances including sulphur and nitrogen oxides. Lead has received much attention (Lazrus et al. 1970; Crecelius and Piper 1973; Edgington and Robbins 1976), largely because of its widespread introduction into the environment from combustion of leaded gasoline. Elevated levels of Pb have been found in many areas distant from vehicular traffic and industry (reviewed by Nriagu 1978; Evans and Rigler 1980; Dillon and Evans 1982). Similar observations have been made for Cd and Zn (Shiomi and Kuntz 1973; Galloway and Likens 1979; reviewed by Nriagu 1980a, 1980b). Furthermore, enrichment of Zn and Cd in the atmosphere relative to crustal abundances (Rancitelli and Perkins 1970; Duce et al. 1975; Jeffries and Snyder 1981) supports the hypothesis that long-range transport of these metals is occurring.

[1]Authors to whom reprint requests should be addressed.

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Deposition from the atmosphere has been shown to be a significant source of Zn and Cd to Lake Michigan (Winchester and Nifong 1971; Robbins et al. 1972; Eisenreich 1980), to the Baltic Sea (Erlenkeuser et al. 1974), and to lakes Huron and Ontario (Kemp and Thomas 1976), of Cd to lakes Superior and Huron (Kemp et al. 1978), and of Zn to Lough Neagh, Ireland (Rippey et al. 1982), and California coastal sediments (Bruland et al. 1974). Since lake sediments are a sink for many trace metals, they have often been used to estimate both natural and anthropogenic deposition (Shimp et al. 1971; Allan 1974; Iskandar and Keeney 1974; Bertine and Mendeck 1978). However, only a few investigators have attempted to quantify storage of these metals in a mass balance framework (Edgington and Robbins 1976; Kemp et al. 1976; Kemp et al. 1978; Nriagu et al. 1979; Robbins 1980; Christensen and Chien 1981). In a few studies it has been suggested that atmospheric inputs alone could account for observed recent (usually the last 100 yr) increases in trace metal content of lake sediments (Edgington and Robbins 1976; Galloway and Likens 1979; Dillon and Evans 1982). However, Edgington and Robbins (1976) and Dillon and Evans (1982) considered only Pb, while Galloway and Likens (1979) calculated the fluxes of several metals to Woodhull Lake from a single core collected from the lake, a practice that in most cases yields very imprecise measurements (Edgington and Robbins 1976; Robbins 1980; Evans and Rigler 1980; Davis and Ford 1982).

We have measured the whole-lake anthropogenic Zn and Cd burdens in 10 lakes in southern Ontario, and by comparing burdens between lakes, tested the hypothesis that the burdens are uniform in the study area. If this were so, it would be likely that atmospheric deposition was the major source of Zn and Cd to these lakes.

Study Area

The 10 lakes studied are located in southern Ontario in Muskoka and Haliburton counties, about 250 km north of Toronto and 200 km southeast of Sudbury, the closest centers of industrial activity. The lakes are situated on the Canadian Shield, an area underlain by Precambrian metamorphic, plutonic, and volcanic silicate rocks that have been substantially affected by glacial processes. The unconsolidated surficial material in the watersheds consists of subglacially deposited tills and, to a much lesser extent, sands and gravels deposited by glacial meltwaters. Peat accumulations are confined to poorly drained pockets often adjacent to the lakes themselves. The soil profile is weakly developed because of the resistant nature of the surficial material and the short period of exposure (about 11 000 yr). In general, the immature soils found in the study area can be classified as brunisolic, podzolic, regosolic, or gleyed (M. Griffith, Ontario Ministry of the Environment, unpublished observations).

The lakes are small (18–93 ha), with mean depths of between 3.3 and 14.2 m and maximum depths of 6–40 m (Table 1). The ratio of the watershed area to lake area ranged from 1.4 to 17.2. The theoretical water replenishment times varied from 1.5 to 11.8 yr. Most of the lakes are dimictic, the exceptions being the two shallowest, Heney and Dickie, which are either very weakly stratified or not stratified at all.

There are no population centers in any of the lakes' watersheds nor any point-source discharge to any of the lakes. There is, however, seasonal use of cottages on the shores of many of the lakes.

TABLE 1. Morphometric parameters for the study lakes (lake area (A_o), mean depth ($\bar{z}$), maximum depth (z_{max}), watershed area (A_d), and theoretical water replenishment time (τ_w = lake volume/outflow discharge)).

Lake	A_o (km^2)	$\bar{z}$ (m)	z_{max} (m)	A_d (km^2)	τ_w (yr)
Blue Chalk	0.494	8.5	23	1.35	5.2[a]
Chub	0.322	8.9	27	2.86	2.2[a]
Clear	0.884	12.5	33	1.24	11.8[b]
Crosson	0.568	8.4	25	5.01	1.9[c]
Dickie	0.932	5.0	12	4.49	2.0[a]
Harp	0.669	12.4	40	5.09	3.2[a]
Heney	0.189	3.3	6	0.72	1.8[c]
Jerry	0.501	12.4	35	8.61	1.5[a]
Plastic	0.315	8.0	16	0.89	4.8[c]
Red Chalk	0.569	14.2	38	6.19	2.5[a]

[a]Four-year average (1976–80; from W. Scheider, Ontario Ministry of the Environment, unpublished observations).
[b]Calculated from Schindler and Nighswander (1970).
[c]Estimates based on long-term average meteorological data.

Methods

Sediment samples were collected during 1979 and 1980 using a K-B gravity corer (Brinkhurst et al. 1969) with clear Plexiglass core tubes having an inner diameter of 4.8 cm. Either two or three cores were retrieved at each of five stations (eight in both Dickie and Red Chalk lakes) per lake. At least one of the five stations was situated such that epilimnetic sediments were obtained.

The cores were sectioned into 1-cm slices to a depth of 20 cm using an extruder and plastic collar (Cross 1977). The two or three replicate slices collected at each site were combined, to provide adequate material for chemical analyses, dried at 100°C to constant mass (a minimum of 24 h), and then ground to a fine powder. A subsample of 0.5–1.0 g of the dried sample was digested overnight at 70°C in a 2:1 mixture of HCl and HNO_3. After dilution with deionized, distilled water, the digestate was analyzed for Cd, Zn, and Pb using a Varian atomic absorption spectrometer (model 1250). All analyses were performed by the Laboratory Services Branch of the Ontario Ministry of the Environment. The standard error of the analyses for all three metals was less than 10%.

Background ("natural") concentrations of Zn and Cd were determined for each site by taking the mean value of the deepest few sections if they appeared to be constant (usually, slices between 17 and 20 cm below the sediment–water interface) and successively adding the next shallowest slice if its concentration was within 1 SD of the mean for all the slices below it. This procedure was repeated until no more slices could be added without exceeding the above rule. In a few cases, background concentrations were apparently not quite reached in the 20-cm slice, in which case the background

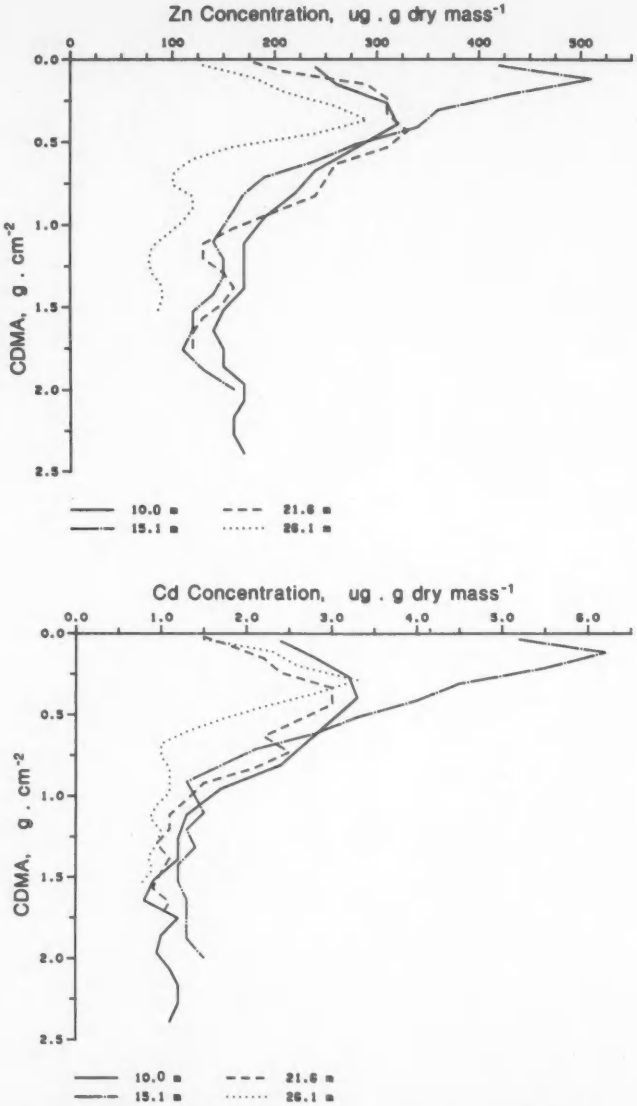

FIG. 1. Zn and Cd profiles from various depths in Clear Lake showing elevated concentrations in recent sediments. CDMA = cumulative dry mass per unit area.

concentration from a core from a similar sampling depth in the lake was used.

Anthropogenic Zn and Cd burdens were calculated by integrating the background-corrected concentration versus depth profile, where depth was expressed as cumulative dry mass per unit area, to take into account sediment compaction (Robbins 1978).

Most of the cores collected were composed of finely textured material (avg. %L.O.I. = 37.1 ± 3.9) with water contents ranging from about 96% in the surface sediments to about 91% at 20 cm below the sediment–water interface (total dry mass to 20 cm = 1.88 ± 0.32 g·cm^{-2}). However, the cores from two epilimnetic sites in Harp Lake and one in both Clear and Crosson lakes consisted of very coarse, dense

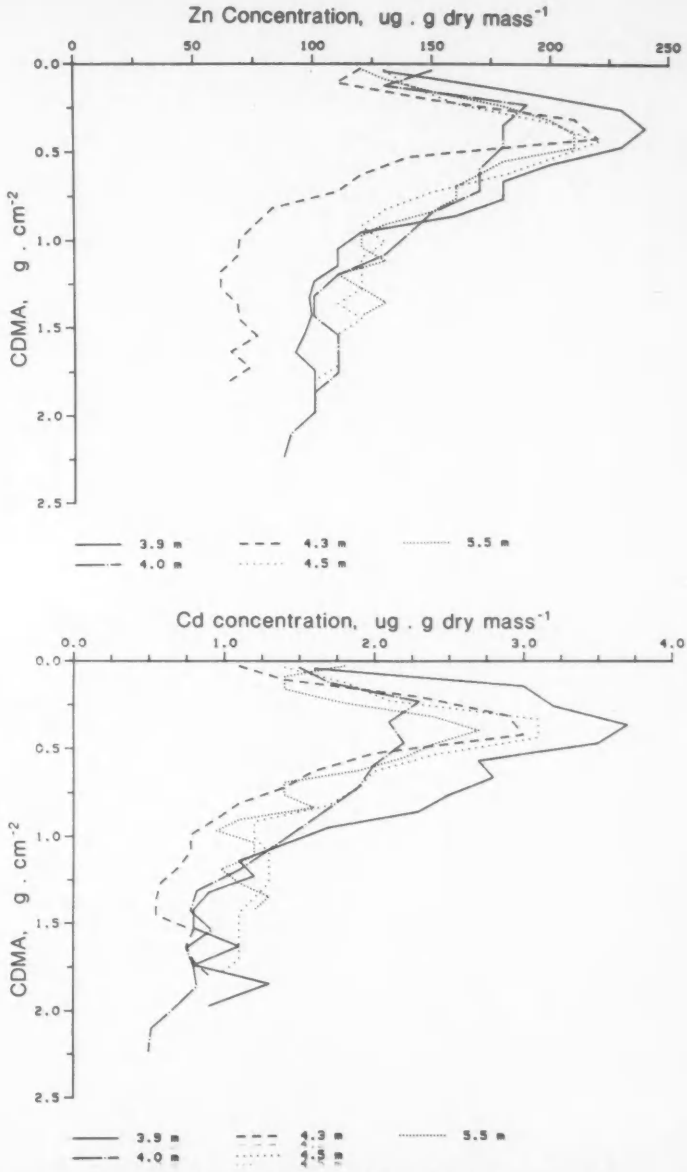

FIG. 2. Zn and Cd profiles from various depths in Heney Lake showing elevated concentrations in recent sediments. CDMA = cumulative dry mass per unit area.

material (total dry mass to 20 cm = 7.50 ± 2.22 g·cm^{-2}) with very low organic content (avg. %L.O.I. = 12.9 ± 8.3). These cores were very different from those collected at all other sites in all lakes. Because the high metal burdens calculated at these four sites depended almost exclusively on their excessive masses rather than high metal concentrations, they were excluded from the following analyses.

The results of the Pb analyses have been reported

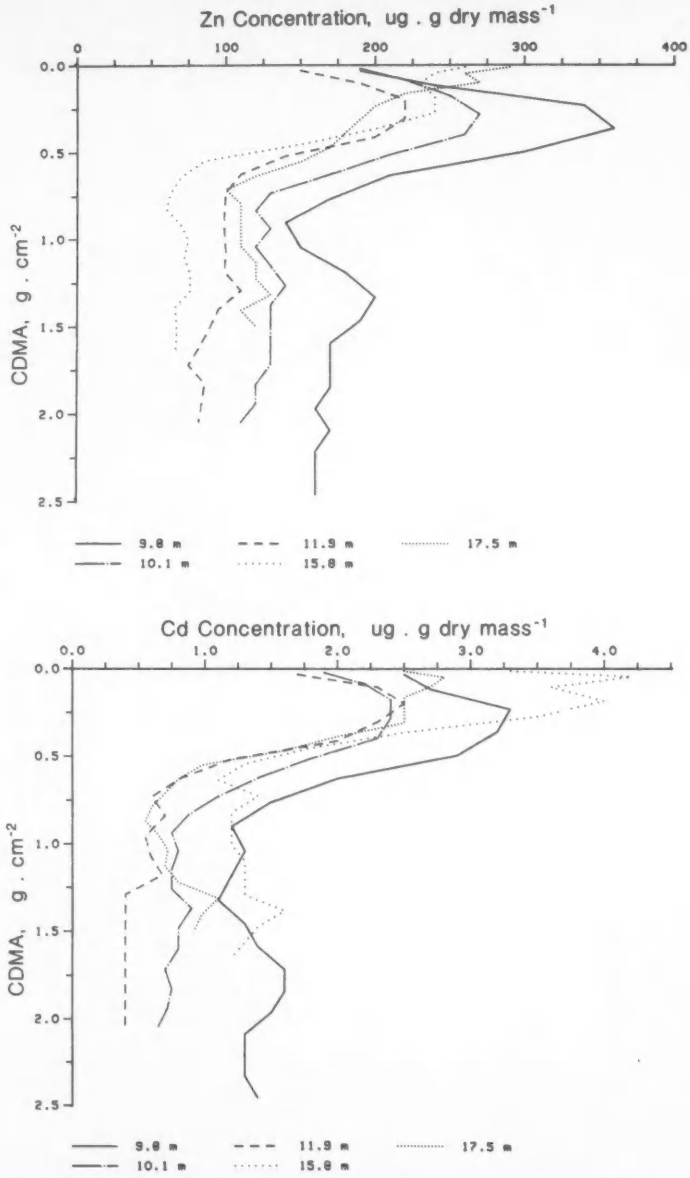

FIG. 3. Zn and Cd profiles from various depths in Plastic Lake showing elevated concentrations in recent sediments. CDMA = cumulative dry mass per unit area.

previously (Dillon and Evans 1982) for 8 of the 10 lakes. Whole-lake Pb burdens (the total anthropogenic Pb content of the lake's sediments averaged over the whole lake area) were measured for Blue Chalk and Harp lakes in a manner identical to that reported for the other eight lakes. Sixty-seven and 107 cores were collected from Blue Chalk and Harp Lake, respectively, and the anthropogenic Pb burdens were calculated at each site. These burdens were integrated over the

whole-lake area to give a whole-lake Pb burden for each lake. The burdens measured in this manner (541 mg $Pb \cdot m^{-2}$ in Blue Chalk Lake and 814 mg $Pb \cdot m^{-2}$ in Harp Lake), were slightly lower and slightly higher than the range (610–770 mg $Pb \cdot m^{-2}$) measured previously in the other eight lakes (Dillon and Evans 1982). The individual whole-lake Pb burdens are used in subsequent calculations.

Results and Discussion

Zinc and Cadmium Profiles

Profiles of the concentrations of Zn and Cd in the sediments of Clear, Heney, and Plastic lakes are shown in Fig. 1–3. Although the peak concentrations of both metals clearly vary from site to site within each lake, it is apparent that, in all cases, the more recently accumulated sediments (approximately 1 $g \cdot cm^{-2}$, or 10 cm below the sediment–water interface) have elevated Zn and Cd concentrations relative to the background levels measured deeper in the cores. All 10 of the study lakes displayed similar elevated levels in the upper layers, with Zn and Cd concentrations being typically 1.4–4.0 times and 1.9–12.5 times greater, respectively, than background levels (Table 2). Elevation of Pb concentration in the recent sediments of the same lakes has been reported (Dillon and Evans 1982); however, peak Pb concentrations were typically two orders of magnitude greater than background levels.

The observed Zn and Cd concentrations in our study lakes were as high as those reported for sediments in some lakes with local and anthropogenic sources. For example, Norton et al. (1978) suggested that the increased use of galvanized iron and municipal effluents were the combined cause of elevated Zn concentrations (200–400 $\mu g \cdot g$ dry $mass^{-1}$) in the sediments of several lakes in New England. Oliver and Agemian (1974) found what they considered to be "anomalously high" Cd concentrations (2.4 $\mu g \cdot g$ dry $mass^{-1}$) in the Ottawa River and Rideau River sediments near the mouth of a small tributary that received drainage from six sanitary sewers. Cadmium levels in all of the Muskoka–Haliburton study lakes were as high or higher. The Zn and Cd concentrations in the recent sediments of the Laurentian Great Lakes are comparable with those observed in this study. Nriagu et al. (1979) reported maximum Zn concentrations of 90–400 $\mu g \cdot g$ dry $mass^{-1}$ and peak Cd concentrations of 2–7 $\mu g \cdot g$ dry $mass^{-1}$ in Lake Erie sediments, while Kemp et al. (1976) reported Zn and Cd enrichment factors of 0.7–3.2 and 0.8–4.6, respectively, in recent sediments in Lake Erie.

Robbins (1980) found that the surface concentrations of Zn and Cd in the sediments of southern Lake Huron were 8–204 and 1.5–4.3 $\mu g \cdot g$ dry $mass^{-1}$, respectively. Kemp et al. (1978) reported similar levels and enrichment factors in Lakes Superior and Huron, while Goldberg et al. (1981) and Christensen and Chien (1981) again measured comparable Zn and Cd concentrations in Lake Michigan (including Green Bay). Zinc and Cd concentrations in the recent sediments of all the Great Lakes and enrichment factors relative to natural levels are comparable with those of the lakes in Muskoka–Haliburton, remote from any point sources. Similar findings have been reported for Woodhull Lake (Galloway and Likens 1979) and Sagamore and Woods lakes (Heit et al. 1981) in Adirondack State Park. These lakes are also remote from any point sources, indicating that long-range transport of Zn and Cd via the atmosphere may be a significant mechanism for input of these substances to lakes.

Whole-Lake Zinc and Cadmium Sediment Burdens

The anthropogenic Zn and Cd burdens were calculated at each site in the study lakes (Table 2). Because the background and peak concentrations of each element varied from site to site within each lake, the calculated burdens also varied spatially within each lake. The observed variation in metal burden calculated within each lake was typically twofold or threefold, with sevenfold occurring in Crosson Lake. Thus, meaningful comparisons between lakes based on individual measurements are impossible as a result of this variability. Unfortunately, sediment budgets in the past have all too often been built on the basis of an exceedingly limited number of sediment cores (Robbins 1980).

Whole-lake trace metal burdens that are a measure of the excess metal in an entire lake rather than the excess metal at a specific site have rarely been measured. Evans and Rigler (1980) measured the whole-lake anthropogenic Pb burden in Bob Lake in Ontario (820 $mg \cdot m^{-2}$) using information collected at 22 sites in the lake. Robbins (1980) calculated the total storage of Cu, Pb, Ni, and Zn from anthropogenic sources in southern Lake Huron, from cores collected at 65 locations, as 75, 250, 105, and 320 $mg \cdot m^{-2}$, respectively. Dillon and Evans (1982) measured whole-lake Pb burdens (34–92 cores per lake) in eight of the current study lakes; finding that the burden was almost constant from lake to lake (610–770 mg $Pb \cdot m^{-2}$), they hypothesized that input occurred only via deposition directly on the lakes' surfaces.

To compare the burdens in the study lakes, and thus to determine if they are different from each other, whole-lake burdens must be calculated. These trace metal burdens may be estimated by averaging the three to eight site-specific burdens for each lake. An alternate approach, however, has been suggested by Evans (1980) for lakes in which the number of sample sites is small. A similar approach was used by Evans and Dillon (1982). Since both the whole-lake Pb burdens and the Pb burdens at specific sampling sites used in this study are known (Dillon and Evans 1982), the ratio of anthropogenic Pb accumulated at each site in the lake to the whole-lake burden is also known. Because it is likely that the anthropogenic Pb, Zn, and Cd are distributed within each lake in a similar pattern (i.e. the correlation between Zn and Cd burdens and Pb burdens in our lakes was 0.66 and 0.68, respectively, for 44 cores, while Robbins (1980) found that the correlation between anthropogenic Zn and anthropogenic Pb in southern Lake Huron was 0.93), then the Zn or Cd burdens that we measured at each site can be prorated according to the Pb ratio.

An example of such a calculation is demonstrated in Table 3. The Pb burdens measured at four of the five sites in Chub Lake were substantially greater (as much as 300%) than the 645 $mg \cdot m^{-2}$ calculated previously on a whole-lake basis using all cores (Dillon and Evans 1982). It is therefore

TABLE 2. Background and maximum concentrations of Zn and Cd in the sediments of the 10 study lakes. Anthropogenic burdens at each site were calculated as the integrated metal content per unit area in excess of the background or natural amount.

Lake	Water depth (m)	Background ($\mu g \cdot g$ dry mass^{-1})		Maximum ($\mu g \cdot g$ dry mass^{-1})		Burden ($mg \cdot m^{-2}$)	
		[Zn]	[Cd]	[Zn]	[Cd]	Zn	Cd
Blue Chalk	8.4	103	0.60	180	1.90	1080	17.5
	12.0	61	0.88	190	2.30	629	3.7
	15.3	100	0.94	210	3.00	1310	23.0
	19.9	95	0.94	200	2.90	895	20.4
	23.0	100	0.94	220	3.00	516	10.4
Chub	6.9	74	0.40	130	1.30	254	8.6
	13.1	83	0.80	190	3.00	695	14.2
	18.4	69	0.80	230	3.30	1260	21.1
	19.9	69	0.82	180	2.40	956	13.1
	23.5	69	0.40	200	2.60	1070	19.5
Clear	10.0	161	1.07	320	3.30	989	17.1
	15.1	128	1.30	510	6.20	1790	22.4
	21.6	136	1.03	330	3.01	1320	12.8
	26.1	84	0.97	290	3.30	863	8.1
Crosson	7.6	83	0.80	120	1.50	161	3.1
	11.4	82	0.62	160	2.00	589	11.2
	12.9	80	0.67	150	2.00	570	10.7
	23.3	80	0.67	200	2.70	1110	22.8
Dickie	8.5	80	0.84	160	2.90	1080	26.9
	8.5	59	0.70	140	2.10	979	15.7
	9.5	85	0.90	180	2.80	984	20.7
	9.9	80	0.84	150	2.70	1530	13.9
	10.3	63	0.56	220	2.80	1500	22.4
	11.0	67	0.74	170	2.60	1190	22.4
	11.2	67	0.74	160	2.60	1080	20.7
	11.2	67	0.74	200	2.50	880	14.5
Harp	15.4	128	0.83	210	2.40	537	12.2
	20.0	110	1.00	220	2.30	1080	10.8
	32.6	107	0.91	270	3.50	991	16.7
Heney	3.9	98	0.89	240	3.70	916	20.0
	4.0	102	0.73	190	2.30	647	12.9
	4.3	68	0.72	220	3.00	652	10.7
	4.5	113	1.10	220	3.10	516	10.3
	5.5	121	1.13	210	2.70	440	6.6
Jerry	11.0	102	0.81	200	2.90	751	19.9
	12.9	98	0.75	200	2.40	1950	30.9
	17.3	99	0.84	220	2.50	734	11.3
	20.2	108	0.98	240	2.70	980	15.1
	32.3	100	0.98	290	3.70	1350	22.7
Plastic	9.8	168	1.35	360	3.30	803	10.1
	10.1	126	0.77	270	2.40	697	9.1
	11.9	92	0.20	220	2.50	577	15.1
	15.8	69	1.29	260	4.20	748	9.4
	17.5	115	0.79	290	2.80	515	7.9
Red Chalk	4.9	127	0.89	240	2.70	1530	24.5
	9.5	90	0.83	190	2.90	862	19.1
	10.3	128	0.89	220	3.00	682	17.1
	14.5	144	0.87	200	2.10	268	7.3
	15.8	127	2.10	260	4.60	1220	7.0
	18.6	203	1.47	240	2.80	117	8.1
	28.0	126	0.94	340	4.20	864	15.6
	34.0	100	1.50	290	5.10	1310	24.7

TABLE 3. Anthropogenic Zn, Cd, and Pb burdens at five sites in Chub Lake, ratio of the whole-lake Pb burden (Pb_{WL} = 645 mg·m^{-2}; Dillon and Evans 1982) to the Pb burden at each site, and whole-lake Zn and Cd burdens calculated using the Pb burden ratios. Standard error (SE) is reported in parentheses.

Water depth (m)	Burden at site (mg·m^{-2})			Pb burden (WL)/ Pb burden (site)	Pb-corrected burden (mg·m^{-2})	
	Zn	Cd	Pb		Zn	Cd
6.9	254	8.6	529	1.22	310	10.5
13.1	695	14.2	1090	0.59	413	8.4
18.4	1260	21.1	1410	0.46	578	9.7
19.9	956	13.1	1380	0.47	446	6.1
23.5	1070	19.5	2020	0.32	341	6.2
Mean	847	15.3	1290		418	8.2
(SE)	(390)	(5.1)			(105)	(2.0)

probable that the Zn and Cd burdens at these sites are also greater than the whole-lake average. If the measured burdens are individually prorated according to the ratio of the whole-lake Pb burden to site Pb burden, then five independent estimates of the whole-lake Zn and Cd burdens are obtained. In Chub Lake, the variability of these measurements (expressed as standard error) is reduced relative to the "uncorrected" values. Furthermore, the Pb-corrected whole-lake Zn and Cd burdens are only 50% of the uncorrected burdens. This is because the calculation of the whole-lake Pb burden takes into account the fact that part of the littoral zone consists of "uncoreable" bedrock or boulders, i.e. no fine sediments are accumulating in portions of the lake.

Similar calculations of whole-lake Zn and Cd burdens were performed for all 10 of our study lakes (Table 4). Uncorrected whole-lake Zn and Cd burdens are, on average, about twice the Pb-corrected whole-lake burdens.

To assess whether the Pb-corrected Zn and Cd burdens provide a better estimate of the whole-lake burdens than a simple average of the three to eight measurements made in each lake, we used a one-way analysis of variance to compare the variability within each of the two methods. The error mean squares were compared using the F-test. The within-lake variability in both the Zn ($P < 0.01$) and Cd ($P < 0.01$) burdens was much less when the Pb-corrected burdens were considered, indicating that these corrected burdens were more precise estimates of the whole-lake burdens than were the simple averages.

Comparison of Zinc and Cadmium Burdens Between Lakes

Each of the Pb-corrected anthropogenic Zn and Cd burdens calculated for a lake is an estimate of the whole-lake burden of that metal. We used two-way analysis of variance to compare the between-lake variability to the within-lake variability in Zn and Cd burdens. There were no significant differences in either Zn or Cd burdens between the study lakes ($F = 0.64$, $P = 0.76$ and $F = 1.17$, $P = 0.34$, respectively).

A similar analysis was carried out on the background concentrations of Zn and Cd in the study lakes. Unlike the anthropogenic burdens of these metals, the background concentrations were significantly different between lakes ($F = 5.64$, $P = 0.00004$; $F = 2.30$, $P = 0.03$, respectively), indicating that either the natural supply of these elements to the lakes or the retention or removal efficiency of these lakes for the two metals is different from lake to lake. However, because anthropogenic burdens are not different, an anthropogenic source must supply the metals equally to all of the study lakes.

TABLE 4. Anthropogenic Zn and Cd burdens in the sediments of the study lakes. Uncorrected burdens are the average of the individual burdens at three to eight sites per lake; Pb-corrected burdens were calculated as in Table 3.

Lake	Uncorrected burden (mg·m^{-2})		Pb-corrected burden (mg·m^{-2})	
	Zn	Cd	Zn	Cd
Blue Chalk	886	15.0	592	7.6
Chub	847	15.3	418	8.2
Clear	1240	15.1	596	7.3
Crosson	607	12.0	322	6.2
Dickie	1150	19.6	488	8.1
Harp	869	13.2	617	9.7
Heney	634	12.1	475	8.9
Jerry	1150	20.0	587	10.4
Plastic	668	10.3	506	7.8
Red Chalk	855	15.4	563	11.3
Mean	900	15.0	530	8.8

The anthropogenic source that fulfils this requirement is atmospheric deposition. If the anthropogenic Zn and Cd burdens in these lakes were the result of deposition from the atmosphere directly on the lakes' surfaces and not a result of input from their watersheds, then there should be no relationship between the relative size of the watershed (i.e. the ratio of watershed area to lake area) and the metal burdens in the lakes. There was, in fact, no significant linear relationship (measured by the coefficient of determination) between A_w/A_o and the whole-lake Zn ($P > 0.5$) or Cd ($P > 0.1$) burden.

Possibly, the study lakes were not equally efficient sinks for Zn and Cd. The retention of these metals may be affected by either physical factors, in particular the water replenishment times of the lakes (see Table 1), or chemical factors. Regression analysis, however, indicated that there was no significant linear relationship between either anthropogenic Zn or Cd burden and water replenishment time of the lakes ($P > 0.4$ for the coefficient of determination).

The chemical factor most likely to affect the retention of metals by the lakes is pH. Dillon (1982) and Dillon and Smith (1982) demonstrated that Zn retention in the sediments of two acidic lakes (pH < 5.0) near Sudbury, Ont., was much less than in three lakes with higher aquatic pH (pH > 6.0). Cadmium mass balances were not measured for the same lakes. At lower pH, possibly a greater proportion of the metal may remain in solution and therefore be lost from the lake by outflow. With the exception of Clear Lake, whose pH ranged between 5.6 and 6.1 during our studies, the other lakes could be divided into two groups (P. Dillon, Ontario Ministry of the Environment, Rexdale, Ont., unpublished observations): one consisting of four lakes whose mean annual pH was always greater than 6.2 (Blue Chalk, Harp, Jerry, Red Chalk) and the other consisting of five lakes with mean pH less than

5.7 (Chub, Crosson, Dickie, Heney, Plastic). A linear comparison of the mean Zn and Cd burdens (590 and 9.75 $mg \cdot m^{-2}$ for the high-pH group and 442 and 7.8 $mg \cdot m^{-2}$ for the low-pH group) between these two groups demonstrated that the differences were statistically significant ($t = 2.08$, $P = 0.045$ and $t = 1.94$, $P = 0.060$ for Zn and Cd, respectively). Thus, a tendency for lakes of low pH to have low metal burdens in the sediments is apparent. This hypothesis warrants further investigation with a larger number of lakes.

We have demonstrated that Zn and Cd concentrations are substantially elevated in the recently deposited sediments compared with natural or background concentrations in 10 lakes in southern Ontario that are remote from any point sources. Maximum concentrations are as great as levels reported for some lakes known to be polluted by local anthropogenic sources.

Whole-lake anthropogenic Zn and Cd burdens were calculated by prorating site-specific burdens according to the ratio of the site-specific Pb burden to the previously measured whole-lake Pb burden. There were no significant differences in Zn or Cd burdens between lakes. It was suggested that there was less efficient sediment retention of Zn in the lakes with low aquatic pH (<5.7) than those with high pH (>6.2). There was no significant relationship between Zn or Cd anthropogenic burden and the ratio of watershed area to lake area or water replenishment time of the lakes, indicating that deposition from the atmosphere directly onto the lakes' surfaces was an important input of these metals to the lakes.

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Analysis of Multiple Objectives in Oregon Coho Salmon Policy

K. D. WALKER

Department of Agricultural Economics, University of Missouri, Columbia, MO 65211, USA

R. B. RETTIG

Department of Agricultural and Resource Economics, Oregon State University, Corvallis, OR 97331, USA

AND R. HILBORN

Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C. V6T 1W5

WALKER, K. D., R. B. RETTIG, AND R. HILBORN. 1983. Analysis of multiple objectives in Oregon coho salmon policy. Can. J. Fish. Aquat. Sci. 40: 580 – 587.

Our objective was to determine whether formal decision analysis could assist fishery managers in Oregon to evaluate alternative strategies with respect to allocation and production of wild and hatchery coho salmon. The method chosen given multiple objectives and uncertainty is multiattribute utility analysis. The analytical model consists of two main components: (1) a computer model that simulates the life cycle of hatchery and stream spawning coho salmon given environmental variation, different hatchery juvenile release levels, and harvest rates and (2) an objective function that evaluates the aggregate levels of catch and escapement resulting from alternative release levels and harvest rates. The approach was used to rank the expected outcomes from 12 proposed policies. We concluded that (1) the most effective policy is achieved with a relatively low harvest rate and high smolt release level, (2) selection of a particular harvest rate is the most important decision variable, and (3) a large smolt release level can be maintained unless such releases adversely decrease the ocean survival of stream spawning coho. If the agency is to be significantly helped, the analysis must be expanded to involve a larger number of decision makers, incorporate additional objectives such as catch variability, and include a finer level of detail in the simulation model.

WALKER, K. D., R. B. RETTIG, AND R. HILBORN. 1983. Analysis of multiple objectives in Oregon coho salmon policy. Can. J. Fish. Aquat. Sci. 40: 580 – 587.

Nous avons voulu dans la présente étude déterminer si une analyse formelle des décisions pouvait aider les gestionnaires des pêches de l'Orégon dans l'évaluation de diverses stratégies de distribution et de production de saumons coho sauvages et d'élevage. Tenant compte de nombreux objectifs et incertitudes, nous avons choisi comme méthode l'analyse de l'utilité d'attributs multiples. Le modèle analytique comprend deux éléments: (1) un programme machine simulant le cycle biologique de saumons coho en voie de ponte en écloserie et dans la nature avec variation de l'environnement, divers niveaux de peuplement de saumoneaux d'élevage et taux de récolte donnés et (2) une fonction objective permettant d'évaluer la somme des prises et de l'échappement résultant d'un choix particulier de peuplements et de taux de récolte. Une telle approche a été utilisée pour classer les résultats anticipés de douze politiques proposées. Nous concluons que (1) un taux de récolte relativement faible et un peuplement abondant de smolts étaient la politique qui donnait le meilleur rendement, (2) le choix d'un taux de récolte est la variable de décision la plus importante et (3) la mise en liberté d'un grand nombre de smolts peut être maintenue, à moins que de tels peuplements ne réduisent la survie en mer des saumons coho se reproduisant dans les cours d'eau. Pour aider de façon significative l'organisme de gestion, il faudra étendre l'analyse de facon à inclure un plus grand nombre de décideurs, des objectifs supplémentaires tels que variabilité des prises et, enfin, un modèle de simulation plus raffiné dans ses détails.

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Oregon Coho Salmon Policy

Policy decisions in fishery management are becoming increasingly complex and difficult. This is especially true for the salmon fisheries where policy outcomes affect the productivity of the salmon resource and the subsequent well-being of commercial fishermen, charter boat operators, Indian fishermen, and sport anglers. Decisions are particularly difficult because of uncertainty in the environment and the conflicting needs and desires of different user groups.

Although salmon management has long been a difficult and frustrating task, ecological, social, economic, and legal factors converged in the late 1970's to create a nearly continuous crisis atmosphere in the California, Oregon, and Washington salmon fisheries (Rettig 1981). Legal and political factors required lower harvest rates of coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawtyscha*). Environmental and biological factors associated with low upwelling reduced the total size of the salmon populations, and a recession, coupled with high interest rates and fuel prices, placed further stress on the commercial troll and net fishing industries as well as economic activities based on recreational fishing. The number of wild salmon has trended downward over the past 20 yr from over a million adults in 1961 to an average of less than half a million from 1974 to 1977 (Oregon Department of Fish and Wildlife (ODFW) 1982). At the same time, the quantity of hatchery smolts released has increased from 7.5 million in 1961 to 61.9 million in 1982. The total number of adult coho generally increased during the 1960's from just over 1 million to more than 3 million, experienced large fluctuations during the 1970's (e.g. from 4.2 million in 1976 to 1.2 million in 1977), and in the past 5 yr has shown a strong downward trend with fewer than 1.3 million produced in 1980, 1981, and 1982. Given the depressed level of wild coho, the recent years of low recruits, and the high number of hatchery smolt releases, both the management of public hatcheries and public policy toward the relatively young private ocean ranching industry had come under strong criticism. The ODFW responded with an expanded citizen involvement program and detailed analysis to identify ways to address concerns related to both salmon and trout (ODFW 1982).

Therefore, this study was designed to determine whether an advanced technique, multiattribute utility analysis (MUA) as formulated by Keeney (1977), could aid decision-making procedure in ODFW. Hilborn and Walters (1977) showed how MUA could be used to address difficult salmon management issues. However, their work was cast in a hypothetical framework. This study is designed to test MUA in an applied setting, with the approach used to analyze harvest rates and hatchery juvenile release strategies for Oregon coho salmon.

Procedural Overview

The analysis was conducted in three steps. First, an objective function, more commonly referred to as a utility function, was formulated. Many factors enter into this function, including management's perception of the needs and desires of the different use groups, historical performance of the resource, legal obligations, and attitude toward risk. Second, a simulation model forecasted the probable outcomes (in terms of variables which are arguments in the utility function) from following alternative policies (measured by variables which reflect, either directly or indirectly, actions under the control of management). Finally, the simulation model outcome was inserted into the utility function to obtain subjective evaluations of the alternative policies and thus to provide insight into the impact of these policies.

To implement and carry out the analysis, several discussions were held with Dr. Harry Wagner, then the assistant chief of fisheries for anadromous fish in ODFW. He has considerable knowledge and experience in fisheries management and policy formulation and has been directly involved in planning, monitoring, and improving the coho salmon resource. Before specifying the objective function, Dr. Wagner was asked to list the user groups in Oregon affected by the coho fishery. The attributes or performance measures of the fishery with which each group would be concerned were then specified. The various levels of attributes were to indicate how much better or worse off a particular group would be. Selection of performance measures to be incorporated into the formal analysis was directly tied to the heavy influence ODFW places in policy formulation on the stock concept (the idea that the fishery is an aggregation of many subgroups of coho salmon each with distinctive characteristics and traits). The stock concept (which was discussed thoroughly in a special December 1981 issue of this journal) was important for two interrelated reasons: (1) to potentially maximize the total production of fish over time and (2) to conserve diversity in the gene pool. These concerns were paramount to policy analysis on coastal stocks and of great significance to decisions relating to stocks in the Columbia River production area.

The Coho Decision Problem

Central to formulation of policy for the coho resource is the concept that there are many subgroups or stocks that should be preserved (ODFW 1982). The clearest distinction between stocks in the mixed fishery is between the wild stocks, which have an egg-to-smolt survival rate of 3%, and the hatchery stocks, which have an egg-to-smolt survival rate of 75% (ODFW 1982). Although smolt-to-adult survival rates are greater for wild than hatchery coho, these differences in early life survival lead to quite different optimal exploitation rates. Recent mixed stock harvest rates have resulted in overescapement to many hatcheries and depletion of wild stocks (ODFW 1982).

Two general policy choices that have provoked controversy are the number of smolts to release and the harvest rate to be maintained (ODFW 1982). Following different policies eventually alters the catch and the escapement of both hatchery and wild stocks. To evaluate the different outcomes from alternative policy strategies, formal specification of objectives and attributes is necessary.

Objectives and Attributes

The main goal of ODFW is to maintain a strong and healthy salmon resource while providing as many benefits as possible

to both present and future user groups (ODFW 1982). Translation of the above goal into a set of objectives allows decision makers within the department considerable latitude in interpreting and providing for the needs of user groups and the coho resource as well. Our first step was to explicitly specify objectives along with attributes that measure performance of the system in reaching the objectives.

For the coho decision problem, Wagner identified two primary objectives for ODFW: maximize catch to user groups and maximize escapement of wild coho back to coastal streams. The latter objective was considered to be important because the long-run health of the coho resource is perceived to depend on maintaining sufficient populations of wild stocks to be used in improving and developing better hatchery stocks (Wagner 1979). That is, wild stocks have adapted to a broader range of environments and possess more diverse traits and characteristics than hatchery coho. Because of this, failure to consider wild stocks in policy formulation could lead to a fishery totally dependent on hatchery production. Moreover, he expressed a concern that the more homogeneous conditions in a hatchery would lead to less diversity in hatchery stocks increasing the risk of losing large segments of the smolt production due to disease or other catastrophe.

For the objectives, two attributes, i.e. average annual catch and wild escapement, were chosen to (1) reflect the degree to which the objectives are met over an extended time horizon (in this case, 20 yr) and (2) facilitate understanding of tradeoffs between objectives and implications from alternative policy strategies.

The Utility Function

Multiattribute utility theory was in turn used to derive a function that quantifies the values the decision maker assigns to outcomes regarding total catch and escapement. Several technical matters had to be resolved. First, we dealt with the overall form of that function. Responses by Wagner established that the attributes were mutual utility independent but not additive independent (as discussed in Keeney and Raiffa 1976). The function to be used is

$$(1)\quad U(C, W) = k_c U_c(C) + k_w U_w(W) + k U_c(C) U_w(W)$$

where

$U_c(C)$ is a function of numbers of coho salmon caught in the ocean,
$U_w(W)$ is a function of numbers of wild spawners,
k_c and k_w are the scaling constants for the single-attribute utility functions $U_c(C)$ and $U_w(W)$, respectively, and
$k = 1 - k_c - k_w$ is the scaling constant for the interdependent portion of the function.

Assessment of the single-attribute utility functions and scaling constants was based on pairwise choices between alternative possible outcomes by Wagner. The derivation, as set forth in Walker (1982), follows the steps in Keeney and Raiffa (1976, p. 219–334), summarized in Keeney (1977), and described intuitively in Hilborn and Walters (1977). The data reveal that Wagner was risk averse with respect to each attribute, i.e. he exhibits concave preferences (Keeney and Raiffa 1976). After the questioning procedure was used to estimate several utility points for each attribute, single-attribute utility functions were estimated by fitting an exponential equation. Responses also led to calculation of the scaling constants and the subsequent value of the utility function used in the analysis

$$\begin{aligned}(2)\quad U(C, W) = {} & 0.60[1.05 - 1.62 \exp(-0.00086C)] \\ & + 0.22[1.3 - 3.4 \exp(-0.0096W)] \\ & + 0.18[1.05 - 1.2 \exp(-0.00086C)] \\ & \quad [1.3 - 3.4 \exp(-0.0096W)]\end{aligned}$$

The Simulation Procedure

The decisions required for coho management as assumed herein can be described as follows. The decision has to be made as to what harvest rate to maintain and how many smolts to release. The consequences of the decision are the resultant average annual catch and wild escapement and the desirability of this outcome as measured by the utility function, eq 2. The determination of a best strategy is complicated by the uncertainty at the time a decision is made and by the significant delays between the decision and the outcome. Uncertainty usually exists as to events that take place during this time interval and are beyond the control of the decision maker. One approach that incorporates uncertainty to provide better estimates of different outcomes over time from alternative policy strategies is simulation modeling.

The discussion of our simulation model for the coho decision problem is divided into four parts. First, we specify the alternative input in terms of strategies or plans. Second, we identify uncertain events and functional models that measure the performance or survival of hatchery and wild coho. For wild coho, one model is used. For hatchery coho, different models are used in concert with uncertain events that are believed to alter their survival. Third, we describe uncertain events by assigning probabilities based on historical data, statistical analysis, and the subjective perceptions of the decision maker. Finally, we describe the simulation model that is used to evaluate the alternative strategies and uncertain events using Monte Carlo simulation.

Alternative Strategies

Twelve alternative strategies were developed for model use. These were based on discussion with Wagner and were chosen to (1) reflect past and anticipated management policies and (2) provide a broad range of possible outcomes, each of which would affect the attributes differently. Table 1 shows the specific content of these plans in terms of harvest rates and smolt release levels.

Biological Models and Uncertain Events

For hatchery coho, specification of a functional model depends on uncertain events that affect survival. Although survival of hatchery coho during the first few months in the ocean is strongly dependent on a number of environmental factors (ODFW 1982), this analysis draws only on an upwelling index developed by Gunsolus (1978). The effects of upwelling on survival are shown in Fig. 1, which illustrates the

data from ODFW (1982) used in the regression equations. Researchers with ODFW have hypothesized that in years of high upwelling (Gunsolus index > 300), there is no evidence of a decrease in survival due to higher smolt releases (ODFW 1982, p. II.Ap.3g-1).

To model performance of hatchery coho in years of high upwelling, we make the assumption that increases in smolt releases do not lead to decreases in recruits. A multiplicative function is expressed (after Peterman 1978) as

$$(3) \quad R_t = \alpha S_{t-1}^{\beta} \exp(u_t)$$

where R_t is the number of hatchery recruits in year t, S_{t-1} is the number of hatchery smolts released in year $t-1$, α and β are production parameters, and u_t is a random error term, normally distributed with a mean 0.0 and variance σ^2. Using data from ODFW (1982), production parameters were estimated to be $\alpha = 0.055$ and $\beta = 1.06$.

In years of low upwelling we model two interpretations of the small data set. One view is that there exist ocean limitations as to the amount of coho that can be supported. If hatchery releases exceed these limits, density-dependent factors, it is argued (ODFW, 1982, p. II.Ap.3f-1 to II.Ap.3f-18), can even lead to a decrease in the total number of recruits. Limitations in the ocean environment have been specified using a Ricker model as

$$(4) \quad R_t = \alpha S_{t-1} \exp(S_{t-1} \cdot \beta + u_t)$$

Again, using data from ODFW (1982) shown in Fig. 1, production parameters were estimated to be $\alpha = 0.114$ and $\beta = -0.0000254$.

The second view modeled is that as the number of hatchery coho continues to increase, the marginal gains in additional numbers of recruits become less. This is expressed using a Beverton–Holt model (Ricker 1975)

$$(5) \quad R_t = \frac{\exp(u_t)}{\alpha + \beta / S_{t-1}}$$

where α is a parameter whose increase measures the replacement level of the stock and β is a parameter whose increase measures the maximum recruits per spawner. The parameters were estimated to be $\alpha = 0.00043$ and $\beta = 7.43$ using data from ODFW (1982).

To model wild coho, we used a Ricker curve based on work by ODFW biologists (ODFW 1982) that reflects a limited amount of freshwater spawning and rearing habitat. The Ricker model (Ricker 1975) is expressed as

$$(6) \quad WR_t = WS_{t-1} \exp(\alpha - \beta WS_{t-1} + u_t)$$

where WR_t is the number of wild recruits at the end of generation t and WS_{t-1} is the number of wild spawners at the start of generation t.

To derive the parameters for eq 6, the function may be written by taking logarithms as

$$(7) \quad \ln(WR_t/WS_{t-1}) = \alpha - \beta WS_{t-1} + u_t,$$

TABLE 1. Alternative plans for the coho salmon problem.

Plan	Harvest rate	Hatchery smolt releases in millions
1	0.65	31
2	0.65	48
3	0.65	60
4	0.69	31
5	0.69	48
6	0.69	60
7	0.75	31
8	0.75	48
9	0.75	60
10	0.80	31
11	0.80	48
12	0.80	60

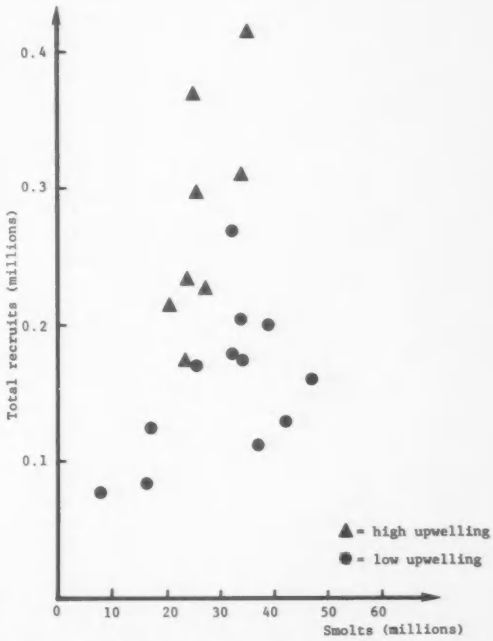

FIG. 1. Relationship between smolts released and total recruits for high and low upwelling years.

which can be estimated by linear regression. Using data developed by ODFW (1982, p. II.Ap.2-4 and II.Ap.3f-3), α and β are estimated as 1.92 and 0.0036, respectively.

Uncertainty enters the calculation of hatchery adults through the existence of two states of upwelling and the possibility of two functional forms when upwelling is low. We introduce another uncertainty by allowing very large numbers of hatchery coho to reduce the ocean survival of wild coho.

In modeling this uncertainty, the idea is to determine the reduction in wild coho based on the degree of belief that hatchery salmon adversely affect wild stocks. To accomplish

TABLE 2. Subjective probabilities of alternative sources of uncertainty in the simulation model.

Alternative[a]	Probability
(A) % occurrence of high upwelling	
(1) 20	0.16
(2) 30	0.34
(3) 40	0.34
(4) 50	0.16
(B) Degree of interaction (C) between hatchery and wild coho	
(1) 0	0.33
(2) 0.35	0.33
(3) 0.75	0.33
(C) Functional model for low upwelling years	
(1) Ricker	0.5
(2) Beverton–Holt	0.5

[a]Total number of alternatives is $4 \times 3 \times 2 = 24$.

this, the reduction in survival of hatchery stocks from larger releases was first determined. The expected rate of reduction in survival (RS) is the percentage reduction in survival that is attributed to increased density due to large smolt releases. As the number of hatchery smolts released increases, RS also increases. To link the effects of increased density of hatchery releases with wild stocks, we defined C as the degree of interaction or correlation such that the higher the value of C the more adverse the impact that hatchery coho will have on wild coho. Then, we multiplied RS by C to get an estimate of the percentage reduction in the wild coho smolt-to-adult survival rate. When upwelling is high, RS = 0 and there is no adjustment to the wild coho survival rate. If there is no belief of interaction ($C = 0$), again no adjustment is made. Finally, if $C = 1$, the expected rate of reduction in hatchery coho survival equals the expected rate of reduction in wild coho survival.[1]

ASSIGNMENT OF PROBABILITIES

The belief that hatchery coho performance during low upwelling years most resembles a Ricker function, or that high upwelling will occur a certain percentage of the time, can be quantified by identifying and assigning probabilities to the range of possible alternatives for each uncertainty. The possible alternatives and corresponding probabilities for the three uncertainties just presented are shown in Table 2. For the specification of uncertainty about upwelling, historical data indicate that high upwelling has occurred 30% of the time in the past 30 yr and 40% of the time in the past 20 yr. To reflect all possibilities, two additional alternatives are used and a normal distribution, which allocates the greatest weight to alternatives 2 and 3, is assumed.

To incorporate uncertainty about the degree of interaction between hatchery and wild coho, three alternatives are considered. Thus, $C = 0$ implies no adverse effects on survival of wild coho due to increased density of hatchery releases, $C = 0.35$ represents moderate effects, and $C = 0.75$ represents severe effects. No evidence was found that would favor one alternative over another. Therefore, equal probabilities are used.

The third uncertainty concerns the functional model for low upwelling years. Initially, we assumed the Ricker and Beverton–Holt models to be equally likely. Alternative probabilities were introduced when sensitivity analysis was conducted.

DEFINITION OF UNCERTAINTY

Define a possible environment or state of nature as a combination of alternatives from each of the three sources of uncertainty. For example, state of nature, θ_j, could be represented as follows: (1) high upwelling occurs 20 percent of the time, (2) $C = 0$ interaction between wild and hatchery coho, (3) performance of hatchery coho in years of low upwelling resembles the Ricker model. The number of states of nature is equal to the product of the sum of alternatives in each uncertainty. In this problem there are $4 \times 3 \times 2 = 24$ states of nature.

The belief that state of nature, θ_j, is the true state of nature is reflected in the probability assignments. Define P_j as the product of probabilities from the alternatives that make up θ_j. All states of nature are adequately represented if and only if $\sum_{j=1}^{24} P_j = 1$.

Before the expected utility from following some alternative plan can be determined, the utility from each state of nature (see Table 2) and plan (see Table 1) must first be calculated. The total combination of plans and states of nature can be represented in matrix form, where the element A_{ij} is the utility of following plan i given state of nature θ_j. A simulation model is used to determine each A_{ij}. Beginning with an initial level of wild coho equal to the most current estimate by ODFW (1982), plan i, state of nature θ_j, and a sequence of random environmental inputs, catch and wild escapement are simulated forward for 20 yr. At the end of the time period, average annual catch and wild escapement are determined. By using a different sequence of random environmental inputs and conducting 10 trials, overall average annual catch and wild escapement[2] are calculated and substituted into the utility function (eq 2). Provided that the outcome, A_{ij}, for plan i and each state of nature, θ_j, has been determined, the overall expected utility (EU) for plan i is

$$(8) \quad \text{EU(plan } i) = \sum_{j=1}^{24} A_{ij} P_j .$$

[1]Regressing the natural logarithm of the ratio of hatchery coho smolts to adults on wild smolts and hatchery smolts explained only 22% of variability in survival and led to a positive sign on the wild smolt coefficient. This result is probably due to measurement error and specification bias. Since this relationship is not investigated in the coho plan (ODFW 1982), we did not include it in our model.

[2]Use of averages of catch and wild spawning escapement is tantamount to selecting a zero discount rate. A more complete treatment of aggregation of data over time would raise several issues, including choice of the appropriate rate of time discount, which have not been discussed in ODFW or in most other fishery agencies (Rettig 1981, p. 152–153).

TABLE 3. Expected utility and expected utility equivalent values for the most preferred management alternatives studied.

	Plans (harvest rate:millions of smolts released)					
	1 (0.65:31)	2 (0.65:48)	3 (0.65:60)	4 (0.69:31)	5 (0.69:48)	6 (0.69:60)
Expected utility	0.7841	0.8196	0.8278	0.7399	0.7573	0.7615
Expected utility equivalent						
Catch[a]	2 254 000	2 520 000	2 591 000	1 990 000	2 087 000	2 112 000
Wild escapement[b]	206 000	229 000	236 000	182 000	191 000	193 000

[a]The certain catch that is equal in value to the uncertain distribution of catch levels resulting from a constant escapement of 200 000 wild spawners.

[b]The certain wild escapement that is equal in value to the uncertain distribution of numbers of wild spawners resulting from a constant catch level of 2 200 000.

The Empirical Results

Prior to determining overall expected utility, plans were examined for dominance across all states of nature. To simplify analysis, plans were examined from two perspectives: (1) plans with similar smolt releases but different harvest rates and (2) plans with different smolt releases but similar harvest rates. In the first category, plans with lower harvest rates dominated plans with higher harvest rates. For example, plan 1, consisting of a harvest rate of 0.65 and smolt release of 31 million, dominated plan 4, which was made up of a harvest rate of 0.69 and smolt release of 31 million. Examining plans with similar harvest rates but different smolt releases revealed that the optimal smolt release relied heavily on whether a high degree of interaction ($C = 0.75$) existed. Excluding those states of nature that assumed a $C = 0.75$ degree of interaction between hatchery and wild coho, higher smolt releases dominated lower releases. However, analysis of only those states of nature with $C = 0.75$ revealed that when high upwelling occurred less than 40% of the time, lower smolt releases dominated higher releases. One explanation why lower smolt releases resulted in higher utility value when $C = 0.75$ was that as smolt releases increased, density also increased and survival of coho decreased. This reduced survival translated into fewer numbers of wild coho and thus lower utility values than for all other states of nature that did not include $C = 0.75$ and high upwelling present 40% of the time.

Partial explanation of the apparent preference for high smolt releases with most of the states of nature was found by analyzing the influence of upwelling on production. The idea was to explore whether, given different percentage occurrences of high upwelling, an optimal smolt release between 31 and 60 million existed. With the Beverton–Holt function, the preferred release, no matter what the percentage occurrence of high upwelling, was 60 million. For the Ricker function, various smolt releases were simulated to determine what release number resulted in the highest average hatchery recruits for different levels of high upwelling. For example, setting the level of high upwelling equal to 30% and using eq 3 and 4, various smolt release levels were simulated forward in time until an optimal release resulting in the highest average hatchery recruits was determined. Of interest for the analysis, when high upwelling was present more than 20% of the time, the most preferred was always a smolt release of 60 million. Thus, within the smolt release range considered and in spite of the maximum release implied by the Ricker function, more smolts were preferred to fewer.

Expected utility values for the top six plans are reported in Table 3. Small differences in expected utility values may be difficult to interpret. For example, the difference in utility between plan 1 (0.8278) and plan 2 (0.8196) is 0.0082. The small changes are due to the assessment procedure, which scales utility between 0 and 1. However, these slight numerical differences may actually reflect significant changes in the levels of the two attributes, catch and wild escapement.

Rausser and Yassour (1981) have suggested an approach to aid the decision maker in interpreting the expected utility values. Specifically, if all attributes except one are held constant at some relevant value, and the certainty equivalent[3] is chosen for the remaining attribute that would generate the expected utility calculated for each policy alternative, analyzing the differences in these "expected utility equivalents" may facilitate the decision making process.

In this case, the expected utility equivalent can be determined by fixing the level of one attribute and, given the expected utility for some plan, solving the utility function for the other attribute. For example, fixing wild escapement at an arbitrarily specified value of 200 000 such that $u_w(W) = 0.8$, and given the expected utility of plan 3 = 0.7841, the utility function (2) is solved obtaining $U_c(C) = 0.817$. Substituting the computed value 0.817 into the single-attribute (conditional) utility function $U_c(C) = 1.05 - 1.62 \exp(-0.00086C)$ results in an expected utility equivalent catch of 2 254 000. A similar procedure is followed to determine the expected utility equivalents of the two performance measures (Table 3).

Expected utility equivalents are helpful in comparing individual performance measures across plans. For example, the expected utility equivalent comparison of catch between plan 2 and plan 3 is a difference of 2 520 000 less 2 254 000 or 266 000 coho. This means that at the level specified for wild escapement and in terms of the utility function (2), the

[3]A certainty equivalent of lottery L (a set of uncertain consequences with probabilities associated with alternative states of the world) is an amount $\hat{x}$ such that the decision maker is indifferent between L and the amount $\hat{x}$ for certain (Keeney and Raiffa 1976).

decision maker should be indifferent between the actual catch in plan 2 plus 266 000 coho and the catch in plan 3. For wild escapement, note that higher smolt releases result in higher expected utility equivalents. This is because all the gains in utility from increased smolt releases translate into increases in the wild escapement equivalent measure. In actuality, increases in smolt releases while maintaining the same harvest rate do not lead to increases in wild escapement; but the gain in catch when translated into utility equivalents for wild escapements more than compensates for the decline in numbers of wild spawners.

Sensitivity Analysis

Sensitivity analysis was conducted to determine how the ranking of alternative strategies changed with different probabilities for each uncertainty and different values for the scaling constants. Initially, the scaling constants were determined as $k_c = 0.6$, $k_w = 0.22$, and $k = 1 - k_c - k_w$. To determine changes in the ranking of plans yet still maintain values of $k_c > k_w$, nine combinations of $k_c = 0.5, 0.6, 0.7$, and $k_w = 0.12, 0.22, 0.32$ were tested. For example, assuming a normal distribution for the different percentage occurrences of high upwelling, equal probabilities for the different degrees of interaction between hatchery and wild coho and equal probabilities for the Beverton–Holt and Ricker functions result in a harvest rate of 0.65 and smolt release of 60 million to be most highly ranked eight times and a harvest rate of 0.65 and smolt release of 48 million to be most highly ranked once.

The empirical results and sensitivity analysis of the coho decision problem suggest the following. First, in terms of the expected utility values, determination of the harvest rate is more important than the smolt release in choosing between alternative strategies. To obtain any real change in rankings, probability distributions had to be used that greatly diverge from what is considered realistic by the staff of ODFW (Walker 1982, p. 54). Maintenance of lower harvest rates[4] (e.g. 0.65) serves to not only protect the diversity of wild coho, but also enables these coho to contribute significantly to the total number of recruits. From the analysis, following plans with high harvest rates (e.g. 0.80) results in the total number of wild coho being severely depleted over time. As a result, utility depends almost entirely on catch from coho produced in hatcheries. Second, the most important factor in determining an optimal smolt release is the percentage occurrence of high upwelling. If high upwelling occurs at least 20% of the time, then a smolt release of 60 million results in the highest average catch. Third, a decrease in smolt releases from 60 million to 48 or 31 million depends on whether a high degree of interaction between wild and hatchery coho occurs. Given the belief that a high degree of interaction does exist, then based on the utility function of the decision maker, release levels of 48 or 31 million should be considered. Finally, in the above analysis a constant smolt release and harvest rate for each plan is used for the entire experiment period. Thus, while the simulation model incorporates uncertainty by using different states of nature, it does not allow for changes in production or harvest as additional information is acquired. As years pass and more is learned about the system adjustments in plans should be considered.

[4]Harvest rates lower than 0.65 would interest researchers. However, rates reported here were constrained to ranges that managers believe to have some political feasibility.

Discussion

This study was conducted to determine whether formal decision analysis could assist ODFW in developing effective policy alternatives with respect to coho salmon. In analyzing the decision problem it became apparent that the dominant issue centered on differences in wild and hatchery coho and how those differences affect policy formulation. As a result, MUA was used to analyze trade-offs between the two stocks and to compare alternative plans consisting of various harvest rates and hatchery smolt releases. Perhaps the greatest benefit of MUA was in isolating major objectives and conflicts, trade-offs, and needed empirical evidence. The process was useful in narrowing down the final list of alternative strategies and promoting discussion of these strategies. MUA was helpful in showing how conflicts could be identified and how consensus solutions could more easily be explored. However, Wagner believes that the analysis must be extended in several dimensions if it is really to enhance policy choice.

For example, Wagner suggests that further work should bring in other decision makers involved in the coho decision problem. Policy choices are not the responsibility of any single individual in ODFW, but rather of a seven-member commission advised both by ODFW and the interested public. By explicitly specifying the objectives of these decision makers, major agreements and disagreements can be identified and alternative policies can be explored. If the decision makers can concur on the wild and hatchery stock issue, MUA can then be used to analyze other objectives and performance measures. For example, in the present analysis the objectives of the user groups are aggregated and measured by the attribute average annual catch. Over an extended time period of 20 yr, the smolt release that results in the highest annual catch is 60 million. However, one drawback of large releases is the additional increase in variation of total recruits (Peterman 1981). Given that entry into and exit from the fishery is not symmetric (i.e. more participants enter after a year of high catch than leave after a year of low catch), many fishermen may be willing to trade higher releases for lower variation. Hence, an attribute that measures variation in catch may be important.

The simulation model could also be enhanced by a more complex analysis of variability. The simulation model used in this paper generates variability in adult production by adding to (or subtracting from) the estimates of wild and hatchery recruits a normally distributed number using the random number generator and the estimated variance in the smolt-to-adult regressions for each stock. While the standard errors used seem reasonable (e.g. the estimated variance for hatchery stock is about one-third of the variance of the random variate, u_t, for wild stocks), direct estimates of the relationship between smolt numbers and the variability of adult production should improve the capability of the model to predict variations in catch over time based on different smolt release policies.

Since different objectives imply trade-offs between user groups, Wagner also recommends involvement of commercial and recreational fishermen, as detailed in Hilborn and Walters (1977). This information can be used to refine the agency's understanding of the needs and desires of the different groups and assist in evaluating and examining policies. Where conflicts arise or where one user group fares poorly, consensus solutions or alternative policies can more easily be developed.

Future work should also disaggregate hatchery stocks. In the present analysis, no distinction is made between public and private hatchery facilities. Consequently, the implied assumption is that all smolts perform equally well. However, because the advent of private facilities is relatively new (first truly large scale releases in 1978), optimal development of stocks to specific hatchery practices is still taking place. To date, the body size of the recruits produced at private facilities has averaged less than those produced at public hatcheries. In addition, research underway at ODFW suggests that private hatchery coho survive at about one-third to one-half the rate of public hatchery coho. Should this conclusion hold true and should production from private hatcheries continue to constitute a substantial portion of total smolt releases, disaggregation of public and private coho and revision of the simulation model is needed. Wagner also suggests that public coho stocks be separated into those originating on the coast and those originating in the Columbia River. This is largely due to the need to consider in-river harvest strategies separately from ocean harvest strategies.

By expanding the objectives and disaggregating the stocks, the analysis could deal more effectively with estimates of monetary benefits and costs. For example, historically, the increase from 48 to 60 million smolts has come from expanded operations at private facilities. Except for minor costs incurred by ODFW to license and set guidelines for the number of smolts that can be propagated at private facilities, the large expenditures for actual production of salmon that eventually become part of a common property resource are assumed by the private sector.

In analyzing production at public hatcheries, large cost differentials exist between facilities. Major factors that affect costs include size, location, species reared, and age of the hatchery. Some hatcheries are outdated, require substantial expenditures for maintenance, and are relatively expensive to operate. Given the large differences in costs and the diverse objectives of the several user groups, analysis of marginal benefits and costs as to hatchery operations and facilities could assist the decision makers in deciding between a release level of 48 or 60 million smolts. Options could include updating the facilities at antiquated hatcheries or phasing out that production and allowing an increase in private production at the same time that restrictions are placed on choice of species and stocks to be reared.

Multiattribute utility analysis is a formal approach to address issues commonly faced by decision makers. The essence of the problem is to make consistent decisions given multiple, and often conflicting, objectives. To that end, recognition and investigation of important performance measures and trade-offs facilitate discussion and analysis of alternative policies and is an integral part of making better decisions. The work reported here suggests that fishery policy can be enhanced by MUA, but that the major contribution is more likely to be a better perception of questions than it is to be a clear statement of answers.

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Optimizing Survey Design for Determining Age Structure of Fish Stocks: an Example from British Columbia Pacific Herring (*Clupea harengus pallasi*)

J. F. SCHWEIGERT AND J. R. SIBERT[1]

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

SCHWEIGERT, J. F., AND J. R. SIBERT. 1983. Optimizing survey design for determining age structure of fish stocks: an example from British Columbia Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 40: 588–597.

Sampling commercial catches of fishes is considered for the first time from the viewpoint of survey statistics. The determination of the age-structure of Pacific herring (*Clupea harengus pallasi*) is approached as a multistage subsampling problem. Optimum allocation of sampling resources is obtained by minimizing the product of total cost and total variance. Optimal survey designs are analyzed for a variety of reasonable cost structures for all age-classes. The most reasonable design that applies to all areas of the coast is to use a two-stage design, including a single sample of about 60 aged fish per vessel. The number of vessels to sample is a function of the required precision and available resources.

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Pour la première fois, est examiné l'échantillonnage des prises commerciales de poisson au point de vue des statistiques de relevés. On détermine la structure par âge du hareng du Pacifique (*Clupea harengus pallasi*) comme s'il s'agissait d'un problème de sous-échantillonnage par étapes. On obtient une distribution optimale des ressources d'échantillonnage en minimisant le produit des coûts totaux et de la variance totale. On analyse diverses conceptions optimales de relevés à coûts raisonnables pour toutes classes d'âge. Un design à deux étapes, comprenant un seul échantillon d'environ 60 poissons d'âge connu par bateau, est celui qui convient le mieux à toutes les régions de la côte. Le nombre de bateaux à échantillonner dépend de la précision requise et des ressources à sa disposition.

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FISHERIES scientists are routinely faced with the problem of sampling fish from commercial catches. There are always constraints on the amount of sampling effort that can be used in a survey. The problem is how to allocate limited sampling resources among loads (vessels), samples within a load and individual fish within a sample. The usual solution is to examine some moderately large number of fish from a convenient number of samples taken from as many loads as the budget will accommodate.

In statistical sampling theory this type of design is referred to as multistage sampling (Chapter 10 of Cochran 1977). Loads are termed "primary units," samples from loads "secondary units," and individual fish "elements." Loads are considered to be random samples from the population of fish. These samples are then subsampled randomly and measurements made on an aliquot of fish from the subsample. Generally, there are considered to be two constraints on survey design. The first relates to obtaining a precise estimate of the variable of interest. The second relates to survey cost. The objective of optimal survey design is to define a survey which either yields the most precise estimate at a fixed total survey cost or determines the least expensive survey design with a fixed total variance estimate. The results for this latter criterion may indicate that the original question which prompted the survey was ill-posed and that the study cannot be done.

The important question of how to determine the most cost effective allocation of sampling resources has not been frequently addressed in the fisheries literature. The purpose of this paper is to present a methodology for designing sampling surveys with an example showing the results of an exploration into the possibility of using standard survey design methods (Cochran 1977; Jessen 1978) to optimize sampling of British Columbia Pacific herring (*Clupea harengus pallasi*) stocks.

Methods

The objective of the herring sampling program is to estimate the proportion of fish in the population at some age. However, age-classes are never uniformly distributed in a population. Therefore an optimal sampling design for one age-class will likely not be optimal for others. Separate optimal designs were calculated for all age-classes in the samples.

The estimation of proportions is treated sketchily in

[1]Present address: South Pacific Commission, P.O. Box D5, Noumea Cedex, New Caledonia.

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most statistical texts on sampling design. We proceed from Cochran's (1977) section 10.5. The mean proportion of fish at age l in the population is given by

$$(1) \qquad P_{l\ldots} = \frac{1}{n}\sum_{i=1}^{n} P_{li\cdot\cdot}$$

while the mean proportion of fish at age l in load i is given by

$$(2) \qquad P_{li\cdot\cdot} = \frac{1}{m}\sum_{j=1}^{m} P_{lij\cdot}$$

and the mean proportion of fish at age l in sample j of load i is given by

$$(3) \qquad P_{lij\cdot} = \frac{1}{k}\sum_{r=1}^{k} a_{lijr}$$

where k is the number of fish from sample j whose ages were determined, m is the number of samples from load i, n is the number of loads sampled, and a_{lijr} is a variable which takes the value 1 if fish $lijr$ is of age l and is 0 otherwise. Note that P_{lij} is thus a binomial proportion. We emphasize that k refers to aged fish only. The number of fish taken in a sample (K) must be somewhat larger (an average of 36% in this case) because many fish cannot be aged due to loss of scales and otherwise poor scale samples.

The variance estimate of $P_{l\ldots}$, derived from Cochran's (1977) equation 10.34, by considering variance to be the weighted sum of terms given in equations 5–7 below is,

$$(4a) \qquad V(P_{l\ldots}) = \frac{N-n}{N}\frac{S_1^2}{n} + \frac{M-m}{M}\frac{S_2^2}{nm} + \frac{K-k}{K}\frac{S_3^2}{nmk}$$

where N is the theoretical number of loads in the population of fish, M is the largest possible number of samples in a load, and K is the number of fish in a sample.

These relations can be greatly simplified because the sampling fractions are negligible, i.e. $N \gg n$, $M \gg m$, and $K \gg k$, so that the variance estimate of $P_{l\ldots}$ is given by

$$(4b) \qquad V(P_{l\ldots}) = \frac{S_1^2}{n} + \frac{S_2^2}{nm} + \frac{S_3^2}{nmk}$$

The estimate for the variance component due to among load variation in age composition is given by

$$(5) \qquad S_1^2 = \sum_{i=1}^{n} \frac{(P_{li\cdot\cdot} - P_{l\ldots})^2}{n-1}$$

while the variance component due to among sample variation is given by

$$(6) \qquad S_2^2 = \sum_{i=1}^{n}\sum_{j=1}^{m} \frac{(P_{lij\cdot} - P_{li\cdot\cdot})^2}{n(m-1)}$$

and the variance component due to among fish variation is given by

$$(7) \qquad S_3^2 = \frac{k}{nm(k-1)}\sum_{i=1}^{n}\sum_{j=1}^{m} P_{lij\cdot}(1 - P_{lij\cdot})$$

which is the expected variance of a binomial proportion.

The total cost of a survey can be expressed as some function of the costs of the individual stages. The usual form of the cost function (e.g. p. 288 of Cochran 1977) is a simple linear equation relating the costs of the sampling stages and n, m, and k,

$$(8) \qquad C = cn_1 + nmc_2 + nmkc_3$$

where C is the total cost, c_1 is the variable cost of obtaining a load, c_2 is the variable cost of obtaining a sample from a load, and c_3 is the variable cost of determining the age of a fish.

The problem is now to determine values of n, m, and k which will provide an estimate of $P_{l\ldots}$ with minimum variance for a fixed cost, or vice versa.

The optimal set of n, m, and k is that which minimizes the product of V times C. Using equations 4b and 8 this product is:

$$(9) \qquad VC = (c_1n + c_2nm + c_3nmk)\cdot\left(\frac{S_1^2}{n} + \frac{S_2^2}{nm} + \frac{S_3^2}{nmk}\right)$$

By the Cauchy–Schwartz inequality (see Kendall and Stuart, 1977, Vol. 1 for a complete discussion; also Raj 1968)

$$(10) \qquad (c_1n + c_2nm + c_3nmk)\left(\frac{S_1^2}{n} + \frac{S_2^2}{nm} + \frac{S_3^2}{nmk}\right) \geq \left(\sqrt{c_1S_1^2} + \sqrt{c_2S_2^2} + \sqrt{c_3S_3^2}\right)^2$$

The product VC will therefore be minimized by the values of n, m, and k which force the inequality towards equality. Expanding both sides of 10 and equating we have

$$(11) \qquad c_2S_1^2m + \frac{c_1S_2^2}{m} + c_3S_2^2k + \frac{c_2S_3^2}{k} + c_3S_1^2mk + \frac{c_1S^3}{mk} = 2\sqrt{c_2S^1\cdot c_1S_2} + 2\sqrt{c_3S_2\cdot c_2S_3} + 2\sqrt{c_3S_1\cdot c_1S_3}$$

Letting:

$$(12) \qquad c_2S_1^2m + \frac{c_1S_2^2}{m} = 2\sqrt{c_2S_1^2\cdot c_1S_2^2}$$

we have:

$$(13) \qquad m^2 - 2m\sqrt{\frac{c_1S_2^2}{c_2S_1^2} + \frac{c_1S_2^2}{c_2S_1^2}} = 0$$

and

TABLE 1. Proportion of fish at age and estimated variance components for Barkley and Nootka Sounds and for combined data, from a three-stage sampling design.

	Age (l =)						
	2	3	4	5	6	7	8
				Barkley Sound			
P	0.139	0.464	0.245	0.094	0.044	0.011	0.002
$S_1^2(\times 10^{-3})$	4.59	5.07	3.46	1.64	0.56	0.19	0.02
$S_2^2(\times 10^{-3})$	1.33	2.98	3.05	0.82	0.71	0.18	0.07
$S_3^2(\times 10^{-3})$	116.20	245.44	182.29	84.21	41.90	10.72	2.11
S_2^2/S_1^2	0.29	0.59	0.88	0.50	1.27	0.95	3.50
S_3^2/S_2^2	87.37	82.36	59.77	102.70	59.01	59.56	30.14
				Nootka Sound			
P	0.024	0.387	0.223	0.173	0.143	0.042	0.024
$S_1^2(\times 10^{-3})$	0.16	12.17	0.48	2.62	2.33	0.12	1.88
$S_2^2(\times 10^{-3})$	0.80	5.57	2.82	3.45	2.68	0.70	7.41
$S_3^2(\times 10^{-3})$	23.38	226.72	173.29	140.55	120.32	40.68	16.60
S_2^2/S_1^2	5.00	0.46	5.88	1.32	1.15	1.67	3.94
S_3^2/S_2^2	29.23	40.70	61.45	40.74	44.90	203.40	2.24
				Barkley and Nootka combined			
P	0.082	0.425	0.234	0.133	0.094	0.027	0.013
$S_1^2(\times 10^{-3})$	5.74	9.34	1.90	3.63	3.97	0.41	0.98
$S_2^2(\times 10^{-3})$	1.07	4.27	2.94	2.14	1.70	0.44	3.74
$S_3^2(10^{-3})$	69.86	236.04	117.75	112.29	81.02	25.66	9.34
S_2^2/S_1^2	0.19	0.46	1.55	0.59	0.43	1.07	3.82
S_3^2/S_2^2	65.29	55.28	60.46	52.47	47.66	58.32	2.50

$$(14) \quad m = \sqrt{\frac{c_1 S_2^2}{c_2 S_1^2}} = m' \quad \text{say}$$

Similarly for k,

$$(15) \quad k' = \sqrt{\frac{c_2 S_3^2}{c_3 S_2^2}}$$

The new variables m' and k' are the values of m and k which will force 10 to equality and thus minimize the product VC. Similar results may be found in Cochran (1977) and Kendall and Stuart (1976, Vol 3).

The optimal number of loads to sample, n', is then dependent on the desired variance

$$(16) \quad n' = \frac{1}{V}\left(S_1^2 + \frac{S_2^2}{m'} + \frac{S_3^2}{m'k'}\right)$$

or the total cost

$$(16b) \quad n' = \frac{C}{c_1 + c_2 m' + c_3 m' k'}$$

The choice between the latter two equations depends on whether the primary constraint is precision (V in equation 16a) or cost (C in equation 16b), respectively. Equations 14 and 15 indicate that the optimal m and k are proportional to the ratio between relative cost and relative error.

In practice, one may find that the among sample variance (S_2^2) is of the same order or smaller than the among load variance (S_1^2) and the two costs involved (C_1, C_2) are roughly equal. This situation will produce a value of m' near 1, indicating that a two-stage sampling design is appropriate. The corresponding equations (from Cochran (1977) Section 10.3)) are given below. The estimated mean proportion at age l in the population is again

$$(1') \quad P_{l\cdot\cdot} = \frac{1}{n}\sum_{i=1}^{n} P_{li\cdot}$$

while the estimated mean proportion at age l in sample i is given by

$$(3') \quad P_{li\cdot} = \frac{1}{k}\sum_{r=1}^{k} a_{lir}$$

The estimate of the variance is given by

$$(4') \quad V(P_{l\cdot\cdot}) = \frac{S_1^2}{n} + \frac{S_3^2}{nk}$$

where n is again the number of loads sampled and k the number of fish to be aged. The among load variance com-

TABLE 2. Optimal sampling design for three-stage sampling for each age-class and a variety of cost estimates. Costs are explained in the text.

		Age (l =)							Cost (1981 C$)		
		2	3	4	5	6	7	8	1	2	3
						Barkley Sound					
1)	m'	1	2	2	2	3	2	4	50	10	0.5
	k'	42	40	35	45	34	35	25			
2)	m'	1	1	1	1	2	1	2	50	25	0.5
	k'	66	64	55	71	55	55	39			
3)	m'	1	1	1	1	1	1	2	50	50	0.5
	k'	93	91	77	101	77	78	56			
4)	m'	1	1	1	1	2	1	2	50	25	1
	k'	47	45	39	51	39	39	28			
5)	m'	1	1	1	1	2	1	2	50	25	2
	k'	33	32	27	36	27	28	20			
6)	m'	4	6	7	5	9	7	13	1500	25	1
	k'	47	45	39	51	39	39	28			
						Nootka Sound					
1)	m'	5	2	5	3	2	5	4	50	10	0.5
	k'	24	29	35	29	30	34	7			
2)	m'	3	1	3	2	2	3	3	50	25	0.5
	k'	38	45	55	45	47	54	11			
3)	m'	2	1	2	1	1	2	2	50	50	0.5
	k'	54	64	78	64	67	76	15			
4)	m'	3	1	3	2	2	3	3	50	25	1
	k'	27	32	39	32	33	38	7			
5)	m'	3	1	3	2	2	3	3	50	25	2
	k'	19	23	28	23	24	27	5			
6)	m'	18	5	19	9	8	19	15	1500	25	1
	k'	27	32	39	32	33	38	7			
						Barkley and Nootka combined					
1)	m'	1	2	3	2	1	2	4	50	10	0.5
	k'	36	32	35	32	31	34	7			
2)	m'	1	1	2	1	1	1	3	50	25	0.5
	k'	57	53	55	51	49	54	11			
3)	m'	1	1	1	1	1	1	2	50	50	0.5
	k'	81	74	78	73	69	76	16			
4)	m'	1	1	2	1	1	1	3	50	25	1
	k'	40	37	39	36	35	38	8			
5)	m'	1	1	2	1	1	1	3	50	25	2
	k'	28	26	28	26	24	27	6			
6)	m'	3	5	10	6	5	8	15	1500	25	1
	k'	40	37	39	36	35	38	8			

ponent is given by

$$(5') \quad S_1^2 = \sum_{i=1}^{n} \frac{(P_{ii.} - P_{i..})^2}{n-1}$$

while the among fish variance component is again

$$(7') \quad S_3^2 = \frac{k}{n(k-1)} \sum_{i=1}^{n} P_{ii.}(1 - P_{ii.})$$

The cost function for the two-stage design is

$$(8') \quad C' = nc_1 + nk\,c_3$$

where c_1 is the cost of obtaining a sample from a load and c_3 is again the cost of aging an individual fish. The estimate of the optimal number of fish to age, k', is derived as before

$$(15') \quad k' = \sqrt{\frac{c_1 S_3^2}{c_3 S_1^2}}$$

and the optimal number of loads to sample is a function of whether the objective is to minimize the variance

TABLE 3. Proportion of fish at age and estimated variance components for Barkley and Nootka Sounds and for combined data from a two-stage sampling design.

	Age (l =)						
	2	3	4	5	6	7	8
			Barkley Sound				
P	0.141	0.466	0.244	0.092	0.45	0.010	0.002
$S_1^2(\times 10^{-3})$	4.88	6.10	3.95	1.80	0.59	0.18	0.02
$S_3^2(\times 10^{-3})$	117.53	244.62	181.59	81.99	42.61	10.17	1.79
S_3^2/S_1^2	24.08	40.10	45.97	45.55	72.22	56.50	89.50
			Nootka Sound				
P	0.026	0.388	0.224	0.171	0.141	0.042	0.008
$S_1^2(\times 10^{-3})$	0.20	13.08	0.56	2.99	2.57	0.11	0.07
$S_3^2(\times 10^{-3})$	25.05	227.80	173.85	140.09	119.17	40.10	7.90
S_3^2/S_1^2	125.25	17.42	310.45	46.85	46.37	364.55	12.86
			Barkley and Nootka combined				
P	0.083	0.427	0.234	0.131	0.093	0.026	0.005
$S_1^2(\times 10^{-3})$	5.94	10.20	2.11	3.90	3.95	0.40	0.05
$S_3^2(\times 10^{-3})$	71.31	236.20	177.71	111.03	80.88	25.13	4.84
S_3^2/S_1^2	12.01	23.16	84.22	28.47	20.48	62.83	96.80

TABLE 4. Optimal sampling design for two-stage sampling for each of a variety of cost estimates.

	Age (l =)							Cost (1981 C$)	
	2	3	4	5	6	7	8	1	3
				Barkley Sound					
1) k'	54	69	74	74	93	82	115	60	0.5
2) k'	60	78	83	83	104	91	129	75	0.5
3) k'	69	90	96	96	120	105	149	100	0.5
				Nootka Sound					
1) k'	121	46	194	75	75	208	113	60	0.5
2) k'	136	51	217	84	83	233	126	75	0.5
3) k'	157	59	250	97	96	269	146	100	0.5
				Barkley and Nootka combined					
1) k'	38	53	100	58	50	86	107	60	0.5
2) k'	42	59	112	65	55	97	119	75	0.5
3) k'	49	68	130	75	64	111	138	100	0.5

$$(16a')\quad n' = \frac{1}{V}\left(S_1^2 + \frac{S_3^2}{k}\right)$$

or the total cost of the survey

$$(16b')\quad n' = \frac{C''}{c_1 + c_3 k}$$

Data used to estimate the variance components were obtained during the herring roe fishery on March 19 and 20, 1974 in Barkley and Nootka Sounds on the west coast of Vancouver Island. The two Sounds are about 100 km apart and are thought to harbour distinctly different stocks of fish. The data consisted of five samples (m = 5) of approximately 100 fish (K = 100) taken from five seine loads (n = 5) in each of the two areas. Accurate cost estimates are surprisingly difficult to obtain. This reflects the diverse nature of the fishery whereby samples for many areas can conveniently be obtained from a few major off-loading sites. Other samples from remote localities may require the efforts of several intermediaries to arrive safely at the processing site. The estimates

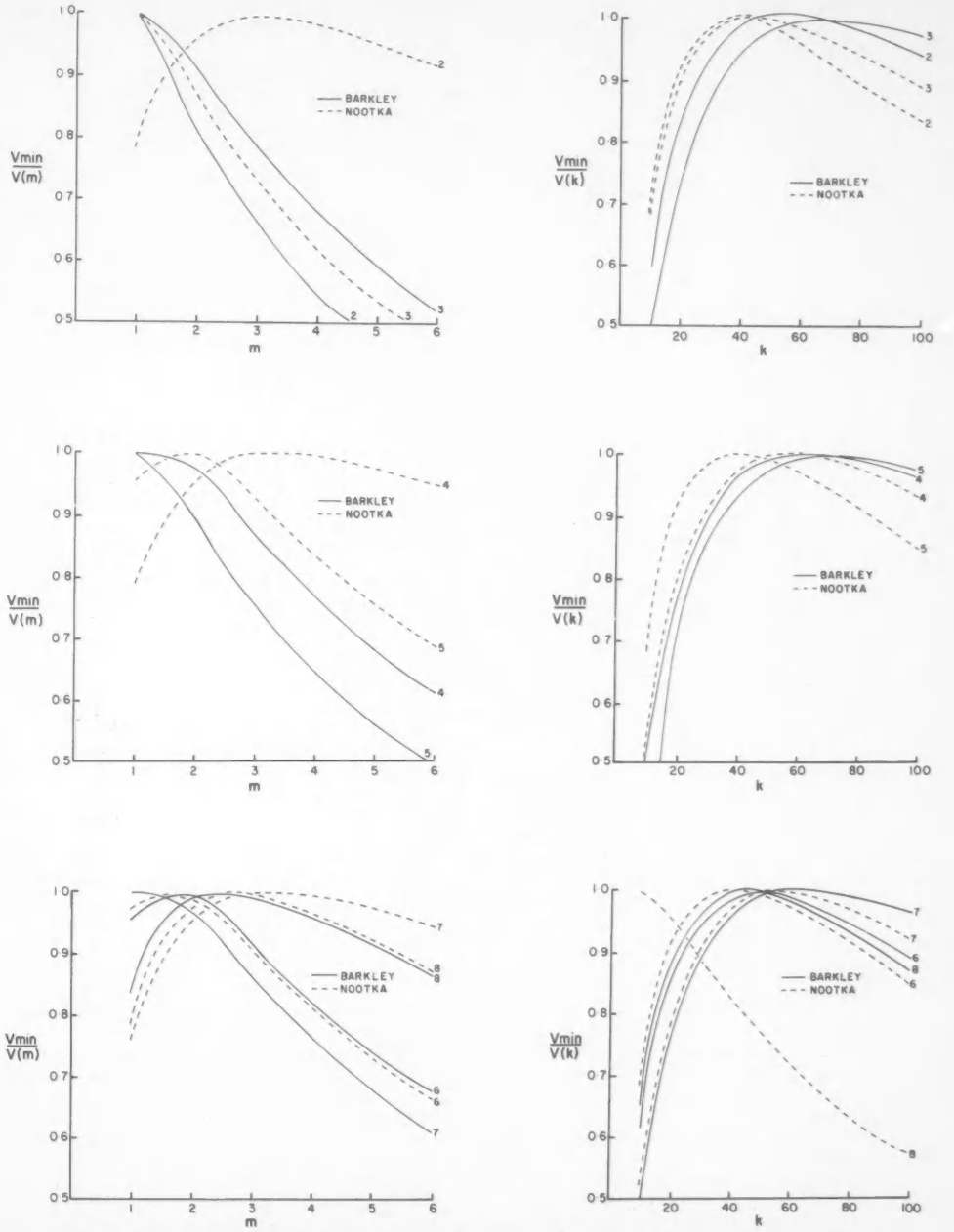

Fig. 1. Variance estimates for a variety of m and k values (V_m, V_k) relative to that obtained at the optimal design (Vmin) for each age-class assuming a three-stage sampling design. Optima as in Table 2 with the second cost structure ($c_1 = 50$, $c_2 = 25$, $c_3 = 0.5$).

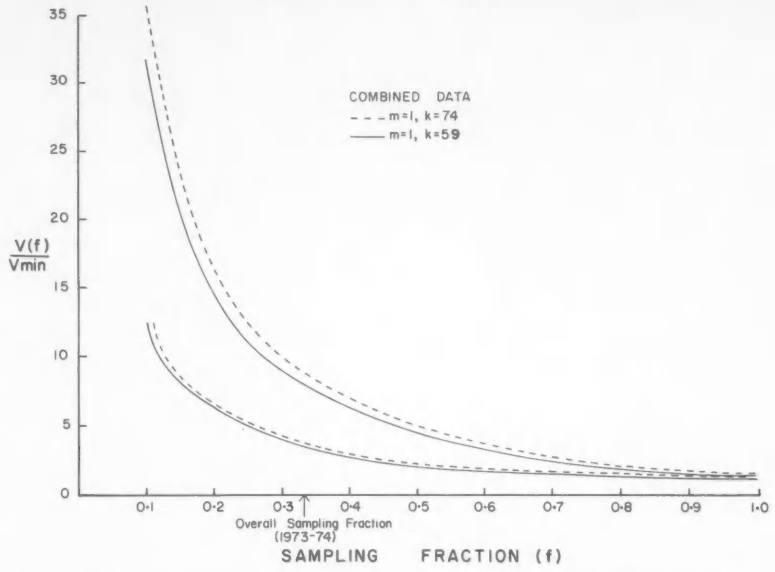

FIG. 2. Variance envelopes obtained for the optimal three-stage design and combined site data at various sampling fractions. The lines represent the range for the most disparate age groups. The minimum variance occurs when all loads are sampled. The dashed line represents the presently utilized sampling design (one sample of 74 aged fish per load).

for c_2 and c_3 used here are based primarily on costs charged by consultants currently employed in sample processing. The most accurate estimate for c_3, the cost of aging individual fish, is 0.5. All costs are in 1981 $C. The best estimate of c_2 is 25. This reflects the salaries and accommodation of port samplers during the fishery plus transportation costs for the samples. The value of c_1 depends on whether a vessel must be chartered specifically to obtain samples (c_1 = 1500) or whether samples can be obtained at a site where commercial vessels are unloading their catch (c_1 = 50). Although it is unlikely that a comprehensive sampling program could be funded if the former situation prevailed we present the results of this cost structure for comparison. We have used a variety of other more reasonable cost structures in the analysis as well.

Results

Age structures and variance components are given in Table 1 for herring in Barkley and Nootka Sounds. The Nootka Sound samples indicate an older age composition than do the samples from Barkley Sound. The largest variance component for both areas and all age-classes is among elements (among fish, S_3^2). The among load component (S_1^2) generally exceeds the among sample component (S_2^2) for Barkley Sound whereas the converse is true for Nootka Sound (Table 1). Pooling data for both areas naturally yields intermediate results.

Optimal three-stage sampling designs for each age-class are presented in Table 2 for several cost structures. Optimal design is clearly a function of age and stock as well as cost. Some general trends are clear. Increasing the cost of obtaining a sample from a load, c_2, decreases m' and increases k' so that the optimal design tends to two-stage. Increasing the cost of obtaining a load, c_1, increases m' so that the designs tend to remain three-stage.

The most accurate cost structure is the second one in Tables 2 and 4. It indicates that Barkley Sound herring stocks are amenable to two-stage sampling for all but age 6 and 8 fish whereas Nootka Sound stocks require three-stage sampling for all but age 3 fish. Pooled estimates indicate that two-stage sampling should be considered. Age structures and variance components appropriate for two-stage sampling are given in Table 3; corresponding optimal sample designs are given in Table 4. Again, as the cost of obtaining a sample, c_1, increases the optimal sample size, k', increases for all age-classes.

Effects of departure from the optimal design can be seen in Fig. 1 and 3. These figures show the precision (variance) of a wide range of sampling designs relative to the variance obtained at the optimal design for each age-class as a function of m and k using the most accurate cost figures, c_1 = 50, c_2 = 25, and c_3 = 0.5. They are all relatively flat in the region of their optima. For Barkley Sound, these curves indicate that most age-classes can be sampled with a variance only 10% over the optimum by a single design: m = 1 and k = 50. For Nootka Sound, the results are not consistant. A three-stage design is suggested for most age-classes with m = 2 and k = 35 or 40. Results for pooled data are not

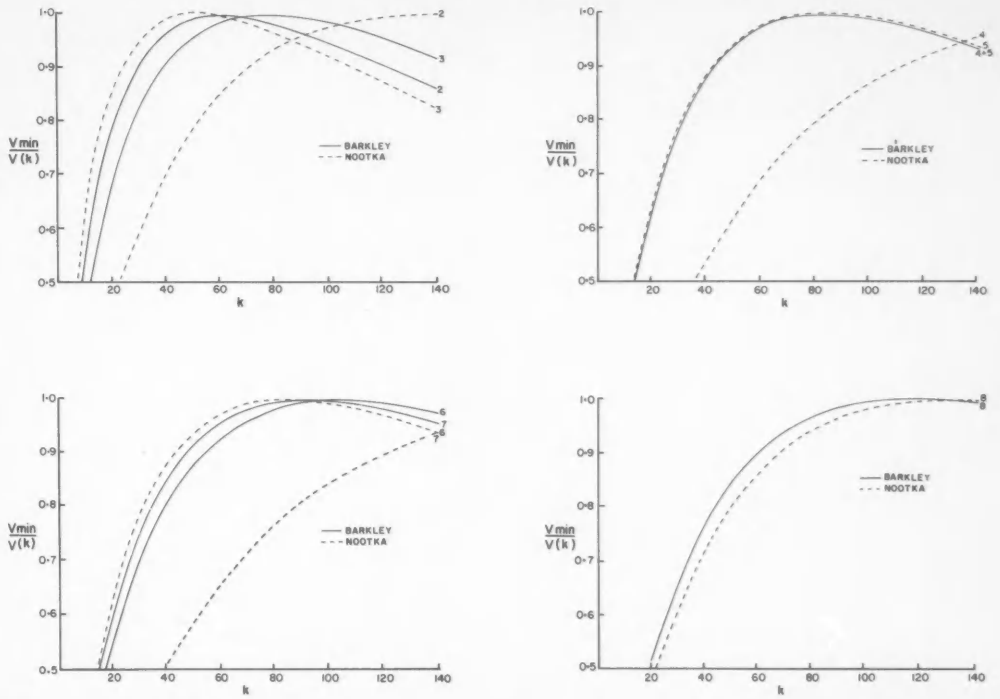

FIG. 3. Variance estimates for a variety of k values (V_k) relative to that obtained at the optimal design (Vmin) for each age-class assuming a two-stage sampling design. Optima as in Table 4 with the second cost structure ($c_1 = 75$, $c_3 = 0.5$).

shown but Table 2 suggests a two-stage design. It should be apparent that not all age-classes can be sampled with equal precision with a single design so some compromise decision regarding which age-classes should be estimated most precisely must be made.

The optimal number of loads to sample, n', will depend on whether one chooses to fix V and minimize C, or vice versa. Assuming one wants to minimize V, Fig. 2 shows the relative precision of sampling as a function of the sampling fraction, i.e. the variance ratio of number of loads sampled (n) to loads in the population of catches (N). These curves are relatively steep and indicate very little improvement after about 30% of the catches have been sampled. Therefore, if the estimated size of a fishery is known beforehand it should be possible to determine how many loads to sample and at what total cost the survey may be done.

On the other hand, if one is interested in minimizing survey cost rather than maximizing precision one can examine the resulting precision of estimates for a given expenditure of funds. Figure 4 shows the ratio between the standard deviation and mean proportion at age (i.e. coefficient of variation) as a function of total cost of sampling. The recruiting age-groups (3 and 4) can be sampled relatively economically whereas the older (rarer) age-classes probably cannot be sampled precisely with any expenditure.

Discussion

Optimal sample designs have been identified for a variety of cost estimates and observed variance structures of Barkley and Nootka Sound herring stocks. These considerations were used to produce optimal designs for every age and stock combination. It is clear from the analysis that without a preliminary sampling effort to estimate variance components for each sampling stage for each age/stock combination it will be impossible to precisely define an optimal survey design. Since such initial sampling will often be too expensive to conduct compromises must be made to permit one to generalize our results.

The first compromise is with respect to age-classes. The analysis (Fig. 4) shows that it may be impossible to sample some age-classes precisely, especially the older, rarer ones. This result is very useful because often the age-classes of most interest, particularly to fisheries managers, are those most recently recruited to the fishery. For herring, these classes are the 3- and 4-yr-olds. If the older fish cannot be sampled precisely, it would be prudent to apply the major effort to the estimation of those ages of greatest importance with the greatest precision. Further, Fournier and Archibald (1982) have shown that pooling older and inaccurately determined age-classes has no adverse effect on, and may even improve,

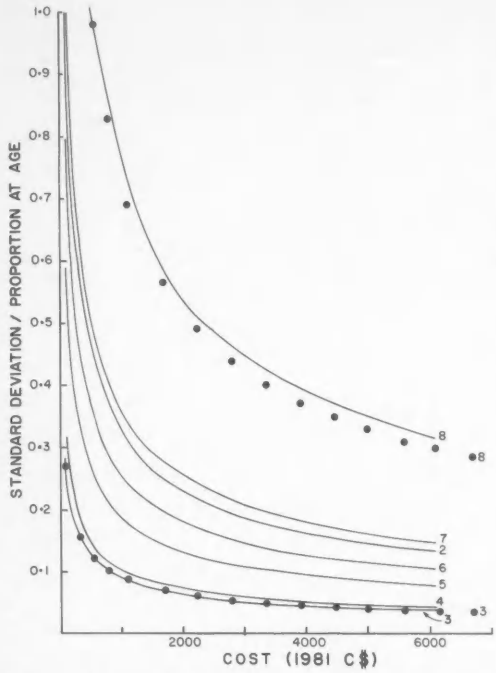

FIG. 4. Estimates of the standard deviation relative to the proportion at age in relation to the total expenditure for the optimal two-stage design determined from the combined site data ($k = 59$). The solid dots represent the envelope obtained with the presently utilized design ($k = 74$).

the performance of age structured population reconstruction models such as sequential population analysis or cohort analysis models.

Our results indicate that two-stage sampling is appropriate for one area, but three-stage sampling is required for another. It probably is not practical to require different designs for different areas since, without an initial sample there is no way of knowing beforehand which design to apply to which area. Further, if different designs are specified for different areas, potential human error is increased. People actually involved in sampling have indicated that multistage designs, particularly those requiring more than one sample per load, may be difficult to apply in practice. Therefore the compromise to make here is to use two-stage sampling for all areas. The consequence of this decision is a decrease in precision in estimating the proportion of certain age-classes and general decreased precision in areas where among sample variance (S_2^2) exceeds among load variance (S_1^2). The compromise optimum is a two-stage design with $k = 59$ (Table 4). In other words 59 fish from a single sample from a load should be aged. We opted to estimate the proportion at age 3 for the combined data with the greatest precision. If it were felt that precise estimates of proportion at age for another age-class were necessary the optimal sample size would be different.

All designs are very sensitive to cost structure. This is apparent from changes in m' and k' in Table 2 and k' in Table 4 with changing cost estimates. The costs used reflect costs as they occur in current practice. Nevertheless there is some uncertainty as to their exact values. The apparently very low cost of processing a sample element c_3, strongly forces the design to two-stage sampling. Also the problem of multiple samples per load does not appear to be adequately treated by the cost function (8); the "difficulty" of obtaining more than one sample per load, mentioned in the previous paragraph, should be reflected in the cost function. We could not determine a satisfactory solution to this problem. Some of these uncertainties could be addressed by considering that "geographical areas" are the primary sampling units. The problem is increased in complexity but uncertainty regarding number of loads and area-specific designs would be eliminated. This approach was not taken because insufficient data exist to evaluate the among area variance component.

Fortuitously, the optimal sample design derived in our study did not differ markedly from that currently in use so no major changes in the sampling strategy for herring were necessary. Should this not be the case costs for redesigning and implementing a new design should also be included in the optimization and evaluation procedure.

There may also be cases in which the simplifying assumptions leading to equation 4b are not justified. Further, complex cost functions, including "penalties" for such complex designs, could be easily written. These two complicating factors may render explicit solutions for m' and k' impossible. Nevertheless, the basic approach is still valid. That is, it is necessary to find values of n, m, and k which minimize the product VC. A number of powerful algorithms are available to find minima in several dimensions (e.g. Nelder and Mead 1965) and these could be applied to the present problem. It is also worth remembering that n', m', and k' must be integers so that extreme accuracy in the solution of these functions is not necessary.

The use of costs to optimize stratified trawl surveys has been discussed briefly by Leaman (1981). Abramson (1968) used a procedure similar to ours to evaluate a stratified subsampling program for shrimp abundance estimation. Otherwise, there are very few published instances of survey optimization for any aquatic ecological application. Most have been in the field of benthic ecology. Saila et al. (1976) used a dynamic programming method to obtain an optimal cost effective method of sampling the bottom of the New York Bight. Cuff and Coleman (1979) used a method similar to the present one to allocate sampling effort in a stratified benthic sampling problem. To our knowledge this is the first attempt to apply a rigorous optimization procedure to the design of fisheries surveys for the estimation of age composition.

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Community Gradients in the Scotian Shelf Zooplankton

M. JOHN TREMBLAY[1] AND JOHN C. ROFF

Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ont. N1G 2W1

TREMBLAY, M. J., AND J. C. ROFF. 1983. Community gradients in the Scotian Shelf zooplankton. Can. J. Fish. Aquat. Sci. 40: 598–611.

The structure of the zooplankton community of the Scotian Shelf was investigated during eight cruises between August 1978 and September 1980. An inshore–offshore community gradient correlated with temperature, salinity, and distance to shore was the strongest pattern revealed by reciprocal averaging. Zooplankton taxa were grouped as inshore (characterized by Arctic species), intermediate (the dominant shelf species), or offshore (expatriate species) on the basis of reciprocal averaging results and correlations with environmental variables. Recurrent group analysis revealed a pattern consistent with that of reciprocal averaging. A shelf recurrent group was always present, dominated by the "core" species: *Calanus finmarchicus, Metridia lucens, Pseudocalanus minutus, Oithona similis,* and *Limacina retroversa*; related shelf edge/slope groups were also present. Substantial differences between cruises were apparent in both reciprocal averaging and recurrent group analysis results and appeared to be related to aperiodic changes in hydrographic conditions. Aperiodic incursions of slope water may represent an energy supplement (as nutrients or zooplankton prey species) or an energy loss if expatriate species exploit the shelf community.

TREMBLAY, M. J., AND J. C. ROFF. 1983. Community gradients in the Scotian Shelf zooplankton. Can. J. Fish. Aquat. Sci. 40: 598–611.

La structure de la communauté zooplanctonique du plateau Scotian a été étudiée au cours de huit croisières, entre août 1978 et septembre 1980. Le résultat de plus important du calcul des moyennes réciproques (RA = Reciprocal Averaging) est un gradient de communautés depuis la côte jusqu'au large, gradient lié à la température, à la salinité et à la distance de la côte. Les taxons zooplanctoniques ont été groupés de la façon suivante : côtiers (caractérisés par des espèces arctiques), intermédiaires (comprenant les espèces dominantes du plateau) et du large (les espèces expatriées), sur la base de RA et de corrélations avec les variables de l'environnement. L'analyse de périodicité des groupements (RGA = Recurrent Group Analysis) donne des résultats comparables à ceux de RA. Il y a toujours récurrence d'un groupement du plateau dominé par les espèces « centrales » : *Calanus finmarchicus, Metridia lucens, Pseudocalanus minutus, Oithona similis* et *Limacina retroversa*; il y a aussi les groupements rebord/talus du plateau associés. Les résultats, tant par RA que par RGA, montrent d'importantes différences entre croisières, différences qui semblent liées à des changements apériodiques de conditions hydrographiques. Des incursions apériodiques d'eau du talus peuvent représenter un supplément (comme nutriments ou espèces proies zooplanctoniques) ou une perte d'énergie si les espèces expatriées exploitent la communauté du plateau.

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THE Scotian Shelf is an area of broad hydrographic and faunal mixing which receives inputs from the northeast (Gulf of St. Lawrence and waters of Labrador Current origin) and offshore (slope water) (Hachey 1937; Houghton et al. 1978; McLellan 1954; Smith et al. 1978). The Scotian Shelf is thus a prime example of what McGowan (1974, 1977) has termed "pelagic ecotones." Within these ecotones, species that have evolved under very different conditions are mixed together, and community structure is determined primarily by advective mixing processes. This is in contrast with the large oceanic gyres which McGowan (1974, 1977) and McGowan and Walker (1979) contend are climax ecosystems and where community structure is determined largely by in situ biological processes.

The few investigations of the Scotian Shelf invertebrate zooplankton, which may be loosely termed "community studies," have been restricted either seasonally or geographically. Studies by Willey (1919) on copepods and Huntsman (1919) on chaetognaths were based on a single summer; Bigelow's (1926) description of plankton distributions was restricted to the extreme southwestern part of the shelf and the Gulf of Maine; Paranjape and Conover (1973) documented the zooplankton composition of St. Margaret's Bay and the extreme inner shelf, and Sameoto and Lewis (1980a, 1980b)

[1]Present address: Department of Fisheries and Oceans, Invertebrates and Marine Plant Division, Halifax, N.S.

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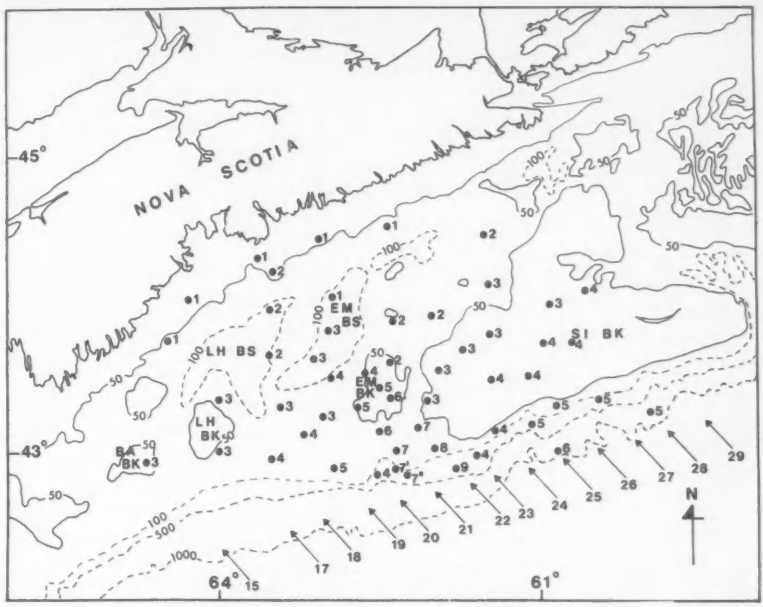


FIG. 1. Study area showing stations sampled between August 1978 and September 1980. Stations are numbered on each transect (shown by numbered arrow). BK, Bank; BS, Basin; BA, Baccaro; EM, Emerald; LH, La Have; SI, Sable. Contours are in fathoms (1 fathom = 1.85 m).

reported summer numbers and biomass of zooplankton at the shelf edge and over the slope.

All these studies recognized an oceanic component in the Scotian Shelf zooplankton. However, none of these studies has quantitatively assessed relationships between zooplankton taxonomic composition and hydrography, nor have relationships among the zooplankton taxa been investigated using multivariate techniques. These procedures for pattern recognition have proved useful in many studies of plankton communities (e.g. Fager and McGowan 1963; Colebrook 1964, 1972, 1978; Angel and Fasham 1973; Shulenberger 1980; Roff et al. 1981).

The Scotian Shelf Ichthyoplankton Survey (SSIP) provided an opportunity to collect zooplankton samples from a wide geographical area throughout the year. Herein we report on the presence of an inshore–offshore community gradient in the Scotian Shelf zooplankton, a gradient characterized both taxonomically and hydrographically.

Materials and Methods

Over a 2-yr period, 201 zooplankton samples were obtained from 53 sampling sites, sampled unequally in the course of eight SSIP cruises: August 9–28, 1978 (39 samples); January 27–February 2, 1979 (24 samples); February 12–27, 1980 (17 samples); May 20–27, 1980 (22 samples); June 12–22, 1980 (22 samples); July 27–August 3, 1980 (19 samples); August 25–29, 1980 (25 samples); and September 11–20, 1980 (33 samples) (Fig. 1). Additional samples, which were obtained at some of these stations for determinations of copepod biomass and production, are reported elsewhere (Tremblay and Roff 1983).

TABLE 1. Summary of RA analysis for each cruise. Data represent percentages of the variance explained by each axis.

Cruise	Axis one	Axis two	Axis three	Total
Aug. 1978	32.5	10.2	7.4	50.1
Jan.–Feb. 1979	14.3	13.7	10.0	38.0
Feb. 1980	25.4	13.9	10.5	49.9
May 1980	31.2	12.8	8.4	52.3
June 1980	30.6	10.9	9.1	50.6
July–Aug. 1980	26.2	13.0	10.9	50.2
Aug. 1980	22.8	10.8	8.7	42.3
Sept. 1980	18.9	12.2	10.0	41.1
Mean	25.2	12.2	9.4	46.8

Samples were obtained with 50-cm SCOR WP-2 pattern nets. These were towed vertically at 30 $m \cdot min^{-1}$ from a maximum depth of 100 m, or from 5 m off bottom if shallower than 100 m. In January–February 1979, additional hauls were taken from 50 m to the surface. Mesh sizes were 250 μm (n = 99), 64 μm (n = 63), 76 μm (n = 34), and 35 μm (n = 5). Samples were preserved in 5% buffered formalin.

All recognizable stages of a taxon were identified by us and checked at the National Museum of Natural Sciences, Ottawa. For the copepods (by far the dominant group), identification included all copepodites of species larger than ~1.5 mm and

TABLE 2. Spearman rank correlations of environmental variables with station scores from the first three RA axes during eight cruises. ROC = rate of change (0–30 m); MD = maximum difference in upper 100 m; * indicates correlation significant at $P < 0.05$; ($16 > n < 40$).

	Aug. 1978 (n = 39)			Jan.–Feb. 1979 (n = 24)			Feb. 1980 (n = 17)			May 1980 (n = 22)		
	1	2	3	1	2	3	1	2	3	1	2	3
Temperature												
0 m	−0.48*	0.16	0.16	0.49*	−0.21	0.18	0.83*	−0.29	−0.19	0.89*	−0.14	0.09
30 m	−0.60*	0.33*	0.22	0.19	0.15	0.24	0.81*	−0.17	0.01	0.65*	0.34	0.22
50 m	−0.47*	0.29	0.28	0.25	0.09	0.39	0.76*	−0.18	0.23	0.82*	−0.04	0.19
100 m	−0.68*	0.16	0.35*	0.70*	−0.17	0.04	0.76*	−0.12	0.02	0.81*	−0.23	−0.11
ROC	0.49*	−0.34*	−0.25	−0.11	−0.01	−0.07	−0.04	0.02	−0.38	−0.18	−0.46*	−0.21
MD	0.03	−0.27	0.12	0.59*	−0.26	−0.07	0.28	0.12	0.47	−0.01	−0.55*	−0.42
Salinity												
0 m	−0.53*	0.19	0.13	0.23	0.05	0.37	0.66*	0.12	0.07	0.69*	0.21	0.22
30 m	−0.67*	0.18	0.11									
50 m	−0.74*	0.14	0.24									
100 m	−0.75*	0.01	0.26									
Density												
0 m	−0.38*	0.21	−0.12	0.20	0.19	0.34	0.56*	0.25	0.08	0.27	0.26	−0.03
30 m	−0.27	−0.36*	−0.14									
50 m	−0.50*	−0.09	0.18									
100 m	−0.68*	−0.18	0.22									
ROC	0.43*	−0.42*	−0.25									
Depth	−0.47*	−0.10	−0.20	0.41*	−0.54*	−0.31	0.07	0.29	0.57*	0.53*	−0.18	−0.48*
Distance to shore	−0.77*	0.17	0.13	0.51*	0.19	0.22	0.33	−0.41	−0.29	0.72*	0.22	0.25
Distance to shelf edge	0.70*	−0.11	−0.23	−0.64*	−0.05	−0.13	−0.33	0.17	−0.18	−0.61*	−0.06	−0.17
Latitude	0.68*	0.18	0.14	−0.77*	0.38	0.25	0.41	0.18	0.45	−0.64*	0.35	0.09
Longitude	0.46*	−0.08	−0.12	0.13	−0.43*	−0.17	0.03	−0.47	0.60*	0.07	−0.79*	0.16

copepodites III–VI of smaller species; nauplii were not identified. Numbers of zooplankters were grouped into broad abundance codes representing a $\log_{10}$ series: 1 = very rare ($<0.5 \cdot m^{-3}$); 2 = rare ($>0.5–5.0 \cdot m^{-3}$); 3 = common ($>5.0–50.0 \cdot m^{-3}$); 4 = abundant ($>50.0–500 \cdot m^{-3}$); and 5 = very abundant ($>500 \cdot m^{-3}$). Correction factors for the various mesh sizes were thus not warranted. Similarly, no correction factor was applied to account for the nets' estimated filtration efficiency of 85%.

Hydrographic measurements at each SSIP station included temperature profiles, using bathythermographs, and surface salinity. During the August 1978 cruise, salinity profiles were obtained at approximately one in five stations, using Nansen bottle samples taken at depths of 0, 30, 50, and 100 m. All salinity determinations were performed using a Guideline autosalinometer (model No. 8400). Tabulated hydrographic data were obtained from the Marine Environmental Data Service (MEDS), Ottawa.

We analyzed the data using reciprocal averaging (Hill 1973), recurrent group analysis (RGA) (Fager 1957), and hierarchical cluster analysis (Wards method, see Wishart 1978). The clustering method was applied only to the August 1978 and January–February 1979 cruise data, and because it confirmed the results of other analyses, it is not discussed further.

Reciprocal averaging (RA) results in simultaneous ordination of species and stations approximately coordinate with one another (Hill 1973). As in principal components analysis (PCA), several axes are extracted from the data, each successive axis accounting for a smaller percentage of the total variance. Reciprocal averaging is better suited for ecological data than PCA, however, because it has greater tolerance to high beta diversity and nonmonotonic variations in species abundance (Fasham 1977; Gauch et al. 1977). To allow some measure of statistical significance to be attached to the species ordinations, Spearman rank correlations were computed between each taxon's abundance codes and the station scores on an axis.

Relationships between species patterns and the environment were assessed by computing Spearman rank correlations between station scores and environmental variables. In addition to temperature, salinity, and density, station scores were correlated with depth, distance to shore and to the shelf edge (100 fathoms = 185-m contour), latitude, and longitude.

Recurrent group analysis is a method for distinguishing nonhierarchical groups of potentially interacting species based on presence/absence data. It has been widely applied in plankton studies (Fager and McGowan 1963; Roff et al. 1981; Shulenberger 1979; Sprules 1975; Venrick 1971) and is used here to corroborate the community patterns revealed by RA. Species were taken to be positively associated if they had an index of affinity greater than 0.5 (see Fager and McGowan 1963).

Prior to the analyses, species occurring only once, and most taxa not identified to species, were omitted from the data set. All computing was performed at the Institute of Computer Science, University of Guelph; RA was run using ORDIFLEX (Gauch 1977), RGA was run using a simple FORTRAN program, and cluster analysis was run under CLUSTAN (Wishart 1978).

TABLE 2. (*Concluded.*)

June 1980 (n = 22)			July–Aug. 1980 (n = 19)			Aug. 1980 (n = 25)			Sept. 1980 (n = 33)		
1	2	3	1	2	3	1	2	3	1	2	3
0.55*	−0.20	0.08	−0.14	0.43	0.29	0.47*	−0.23	0.05	0.42*	−0.32	−0.29
0.72*	0.09	0.24	−0.08	0.75*	0.19	0.55*	0.01	−0.01	0.56*	−0.55*	−0.40*
0.75*	0.11	0.22	−0.09	0.47*	−0.18	0.79*	−0.10	−0.06	0.47*	−0.50*	−0.23
0.85*	−0.26	−0.04	−0.63*	0.30	−0.10	0.40	−0.29	0.38	0.18	0.10	−0.05
−0.25	−0.22	−0.29	−0.05	−0.63*	−0.12	−0.42*	−0.08	0.09	−0.51*	0.54*	0.39*
−0.16	−0.19	−0.19	0.06	−0.26	0.22	−0.36	0.06	0.15	−0.20	0.23	−0.09
0.48*	0.33	0.12	−0.64*	0.37	−0.15	0.72*	−0.35	−0.25	0.69*	−0.50*	−0.26
0.35	0.31	0.13	−0.42	0.11	−0.25	0.15	−0.02	−0.32	0.64*	−0.50*	−0.08
0.66*	−0.46*	−0.12	0.58*	0.28	−0.00	0.06	0.35	0.75*	0.16	0.55*	−0.15
0.62*	0.20	0.18	−0.25	0.79*	−0.04	0.80*	−0.23	−0.23	0.51*	−0.58*	−0.18
−0.49*	0.00	−0.30	0.20	−0.67*	0.24	−0.61*	−0.05	0.14	−0.52*	0.43*	−0.06
−0.60*	−0.29	0.14	−0.14	0.52*	−0.16	−0.50*	0.22	0.05	0.01	0.00	−0.00
−0.04	−0.54*	0.10	0.71*	0.28	0.02	−0.60*	−0.39	−0.38	0.57*	0.79*	−0.12

Results

The greatest proportion of the variance in zooplankton taxonomic composition was related to an inshore–offshore gradient. The inshore end of the gradient was characterized by lower temperatures and salinities and the offshore end by higher temperatures and salinities. The first RA axis accounted for a mean of 25.2% of the variance (Table 1) and was usually defined in terms of both station location and hydrography (Table 2; Fig. 2). For six of the eight cruises (August 1978, January–February 1979, and May, June, August, and September 1980), axis one was significantly correlated with distance to shore as well as temperature and/or salinity (Table 2). In February and July–August 1980, axis one was correlated with hydrographic variables but not with distance to shore (Table 2). During these cruises, the central shelf (Emerald Bank and Basin) was more "offshore" in community character than either the eastern or western shelf (Fig. 2c, f), confounding any correlation with distance to shore. The greater "offshore" character of the central shelf is also evident in most other cruises (Fig. 2b, d, e, h), but because most stations sampled were in the central shelf, the correlation with distance to shore was significant.

To obtain a ranking of taxa in relation to the inshore–offshore gradient, only the three cruises with the strongest horizontal gradients in taxonomic composition and hydrography were considered; these constituted a natural statistical group. In the analyses of August 1978, May 1980, and June 1980, RA axis one accounted for at least 30% of the total variance (Table 1). Most taxa were not present in all cruises, and therefore, mean ranks using all the cruises would severely reduce the number of species considered. The 32 taxa (of a total of 72 identified) common to the three cruises were first ranked within each cruise based on their scores on RA axis one. The correlations between the ranks for each cruise were significant, and the ranks were then averaged (Fig. 3).

These "averaging rankings" were then divided into inshore, intermediate, and offshore groups (Fig. 3), with the aid of the Spearman rank correlations between taxa abundance codes and station scores. Inshore species (e.g. *Temora longicornis*) tended to be negatively correlated with temperature, salinity, and distance to shore; offshore species (e.g. *Clausocalanus* sp.) tended to be positively correlated with the same variables; the intermediate species (e.g. *Oithona similis*) tended to lack significant correlations with the station scores.

Recurrent group analysis revealed a pattern similar to that of RA. A shelf recurrent group was always present, generally comprising most zooplankton species. In addition, there was usually a group(s) of taxa which predominated at the shelf edge or over the slope. Figures 4 (August 1978) and 5 (January–February 1979) indicate the range in complexity of zooplankton groups found in the eight cruises on the Scotian Shelf and upper slope. The many connections in Fig. 4, signifying affinities between species of different recurrent groups, indicate a community continuum over the shelf and upper slope rather than discrete noninteracting communities.

A summary of the relationships between species pairs over the eight cruises, as indicated by RGA, is shown in Table 3. Taxa that were often part of the shelf recurrent group are concentrated in the upper half of Table 3. *Calanus*

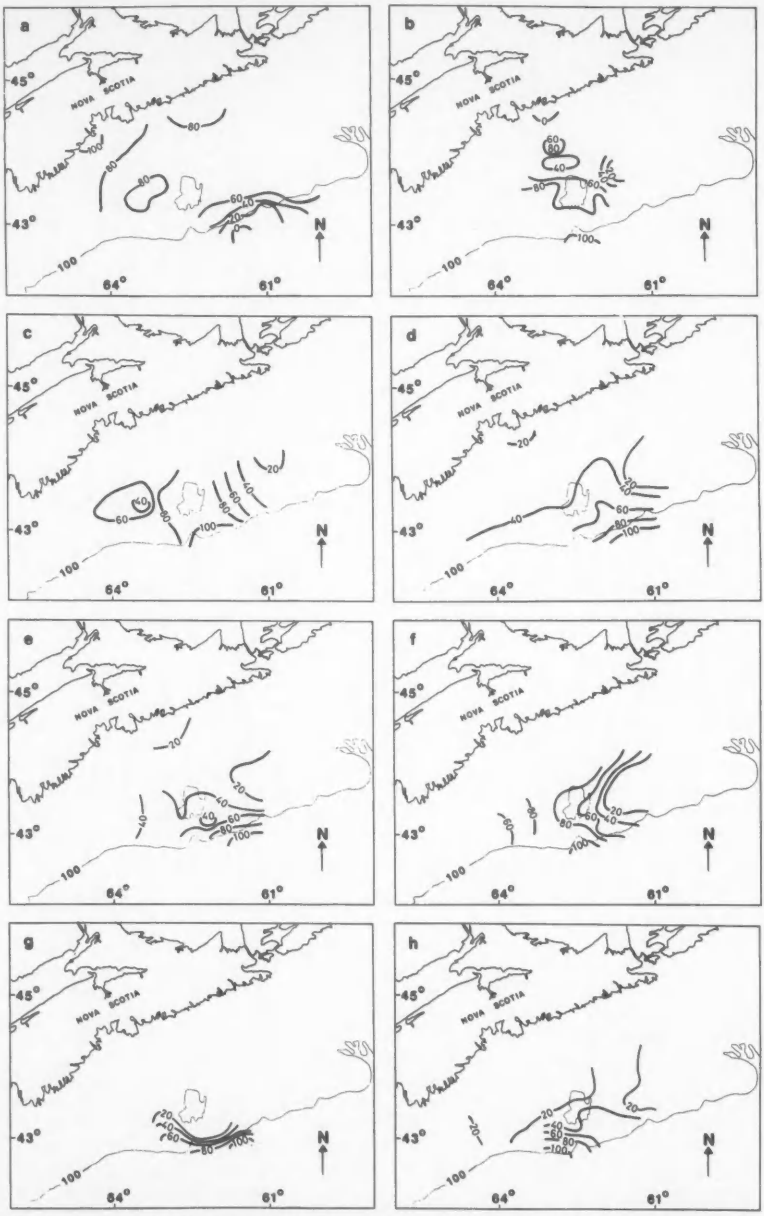


FIG. 2. Contours of station scores on RA axis one. (a) August 1978 (n = 39); (b) January–February 1979 (n = 24); (c) February 1980 (n = 17); (d) May 1980 (n = 22); (e) June 1980 (n = 22); (f) July–August 1980 (n = 19); (g) August 1980 (n = 25); (h) September 1980 (n = 33).

finmarchicus, *Metridia lucens*, *Pseudocalanus minutus*, *O. similis*, and *Limacina retroversa* can be considered the "core species" comprising the shelf recurrent group, since they were positively associated with one another during

every cruise. In the lower half of Table 3 are found taxa which were part of or associated with the shelf edge/slope recurrent group present during at least one of the cruises. Recurrent groups in the shelf edge/slope region were variable in composition; the greatest number of positive affinities between any pair of taxa was three, between *Nannocalanus minor* and *Centropages bradyi*.

Variability in the Strength of the Inshore–Offshore Gradient

Between 14 and 32.5% of the total variance during the eight cruises is explained by RA axis number one (Table 1). A seasonal trend in the strength of the zooplankton gradient was evident in 1980 (Table 1) when it was strongest in May and June and became progressively weaker in succeeding months. However, strong interyear differences were apparent. In August 1980 the first community gradient explained only 22.8% of the variance, while in August 1978 the first RA axis explained 32.5% of the variance, more than in any other cruise.

Only a small proportion of this variability between cruises can be attributed to differences in the number and position of stations. When the August 1978 data set was reduced such that the station composition was similar to August 1980, the variance explained by RA axis one increased to 34.8%.

Much of the cruise to cruise variability in gradient strength appears to be related to unsystematic differences in the prevailing hydrographic conditions. We compared the cruise with the strongest inshore–offshore gradient (August 1978) and contrasted this with the cruise with the weakest gradient (January–February 1979).

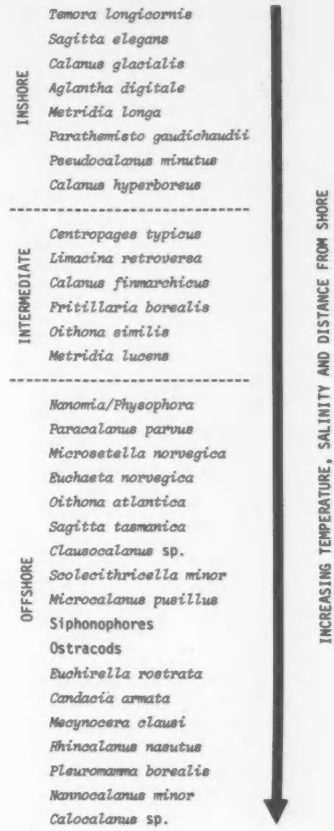
During August 1978 a complex of four zooplankton groups was present according to RGA: a shelf group and three shelf edge/slope groups (Fig. 4). Most zooplankton taxa were either positively or negatively correlated with the inshore–offshore gradient and were ordinated in this manner by RA (Table 4).

The sharpest transition in zooplankton composition occurred just beyond Emerald Bank (Fig. 2a), paralleling abrupt increases in surface salinity and subsurface temperature (Fig. 6).

In January–February 1979, the distinction between inshore and offshore zooplankton was not so clear. Although RGA indicated the presence of a shelf recurrent group which shared 75% of its taxa with the August 1978 shelf group, there were important differences. Four copepods (*Microcalanus pusillus*, *Clausocalanus* sp., *Pleuromamma borealis*, and *Candacia armata*), which in August 1978 were members or associates of one of the shelf edge/slope groups (Fig. 4), occurred on the shelf frequently enough in January–February 1979 to become members or associates of the shelf group.

The mixing of inshore and offshore zooplankton on the shelf in January–February 1979 is corroborated in several ways by RA: the intermediate scores of the four copepod species mentioned above (Table 5), the small number of significant correlations between taxa abundance codes and the station scores (Table 5), and the anomalously high station scores in the central shelf (Fig. 2b).

It is also clear that hydrographic conditions on the shelf were more mixed in January–February 1979 due to a greater influx of offshore waters. Compared with August 1978, the 32‰ isopleth extended much farther shoreward in January–February 1979. In the central shelf, temperatures below 50 m were generally 2°C warmer than in August 1978. In January–February 1979, a retrograde subsurface front was present, indicating an incursion of deeper slope water (Fig. 7).



	June '80	Aug. '80
May '80	0.74*	0.65*
June '80	-	0.76*

FIG. 3. Ecological classification of zooplankton on the Scotian Shelf based on Spearman rank correlations of taxa with station scores. Taxa rankings are derived from average ranks on RA axis one within the three cruises. Correlations (R^2) of species ranks between cruises are shown ($*P < 0.05$).

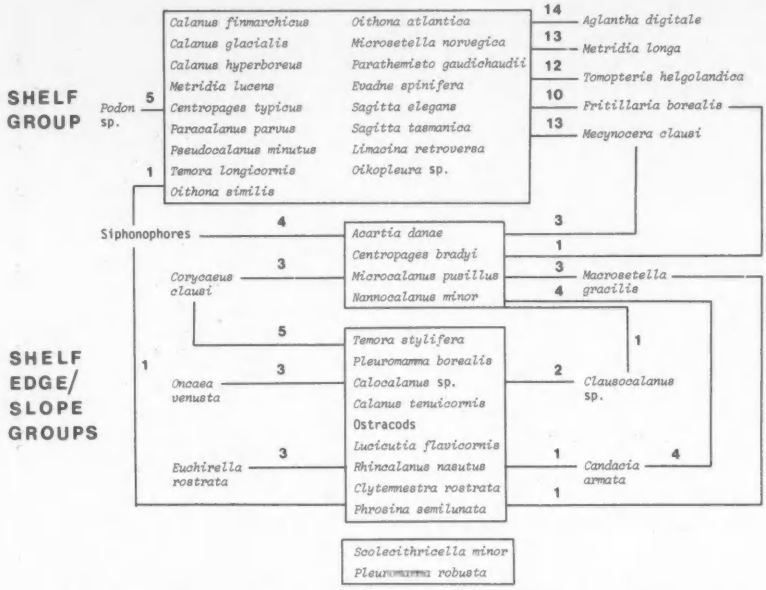


FIG. 4. Recurrent groups of zooplankton on the Scotian Shelf during August 1978. Taxa within a box all have an index of affinity ≥ +0.5; taxa joined to a box are associates with number of affinities shown.

It seems possible that some of the offshore zooplankters found on the shelf in January–February 1979 arrived via this deeper slope water, thus implying a vertical dimension to the inshore–offshore gradient in zooplankton. It was expected that the abundance codes for offshore species derived from 100-m hauls would have been greater than those derived from 50-m hauls. Of six taxa tested (Wilcoxon signed rank test), only siphonophores were more abundant in the 100-m hauls. Five other taxa (not tested) occurred exclusively in the 100-m hauls.

Secondary Community Gradients

The second axis of RA explained a mean of 12.2% of the total variance, considerably less than axis one (Table 1), and was more difficult to interpret. In half the cruises (January–February 1979, May 1980, June 1980, and September 1980), axis two was correlated with longitude and/or depth and seemed to represent an east–west gradient in zooplankton composition (Table 2). In the analyses of several of these cruises, however, taxa characteristic of the eastern shelf on axis two were the same as those characteristic of inshore conditions on axis one. For this reason it seems axis two was related to axis one, even though they were never significantly correlated.

The third axis of RA explained a mean of 9.4% of the variance (Table 1) and was less interpretable than axis two. In the analyses of five cruises (August 1978, January–February 1979, June 1980, July–August 1980, and September 1980), axis three was either correlated with axis one or lacked significant correlations with any of the environmental variables (Table 2). No further attention will be given to interpretation of RA axes beyond the first.

Discussion

The inshore–offshore gradient was the strongest pattern within the zooplankton of the Scotian Shelf. Although it did not explain a large fraction of the variance (mean 25%), this is the first time such a compositional gradient has been quantitatively documented here and characterized by the common zooplankton taxa.

Various ecological classifications have been applied to marine zooplankton, e.g. neritic, intermediate, or oceanic; southern, temperate, or northern; indigenous or expatriate, etc. There is some overlap of these terms depending on the area studied.

Inshore Taxa

The term "neritic" was not used because species recognized as typically neritic in the Bay of Fundy and Gulf of Maine by Fish and Johnson (1937) and Legare and MacLellan (1960) such as *Acartia longiremis*, *A. hudsonica*, *Eurytemora* sp., *Centropages hamatus*, and *Tortanus discaudatus* were either absent or very infrequent in our study. This is not surprising given that all samples were taken more than 10 km from shore; Paranjape and Conover (1973) reported most of these neritic species as important in St. Margaret's Bay. *Temora*

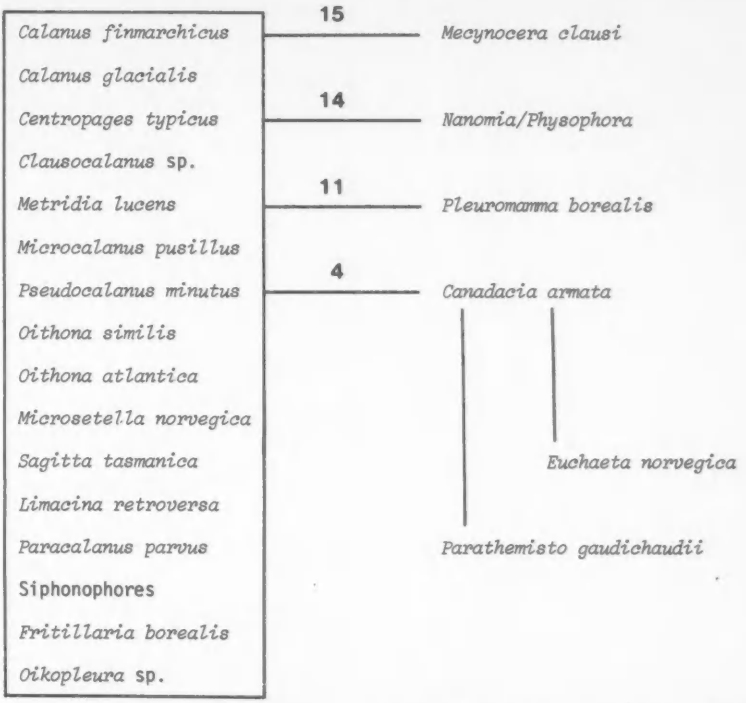


FIG. 5. Recurrent groups of zooplankton on the Scotian Shelf during January–February 1979. Taxa within a box all have an index of affinity ≥ +0.5; taxa joined to a box are associates with number of affinities shown.

longicornis, the most "inshore" species in Fig. 3 and often abundant near shore (Paranjape and Conover 1973; Poulet 1978), also appears to tolerate shelf conditions. Collins and Williams (1981) grouped *T. longicornis* with *C. hamatus* and *A. clausi* as euryhaline marine (27–35.5‰).

Other species grouped as inshore in Fig. 3 were: *Sagitta elegans*, *Calanus glacialis*, *Aglantha digitale*, *Metridia longa*, *Parathemisto gaudichaudii*, *P. minutus*, and *Calanus hyperboreus*. Most of these species were classified as boreal or arctic by Briggs (1974), Colebrook (1964), Fish and Johnson (1937), and Grainger (1963). Fraser (1961) and Colebrook (1964) classified *M. longa* and *C. hyperboreus* as northern oceanic. It appears that on the Scotian Shelf, these species arrive mainly from the northeast rather than from offshore waters. Cox and Wiebe (1979) reached the same conclusion concerning the origin of *C. hyperboreus* in the mid-Atlantic Bight.

The characterization of inshore conditions by arctic species on the Scotian Shelf is undoubtedly related to the cold water of Gulf of St. Lawrence and Labrador Current origin which floods the shelf from the northeast. This water retains its temperature–salinity characteristics most strongly on the inner and eastern parts of the shelf (Houghton et al. 1978; McLellan 1954), explaining the greater "inshore" character of the zooplankton found on Sable Island Bank (Fig. 2). In the Emerald Bank and Basin area (i.e. the Halifax section) water from the northeast is diluted approximately 40% by slope water (Houghton et al. 1978).

Some assessment can be made of whether the taxa in Fig. 3 are indigenous or expatriate (using the definition of Cox and Wiebe 1979). Indigenous species are those for which the shelf is part of the home range or those which breed successfully and maintain healthy populations but are dependent on inocula from another area for long-term stability. Expatriate species include those which die off in shelf waters before reproduction and those which achieve individual and population growth during part of the year but which fail to complete their annual cycle.

Most of the inshore species are probably indigenous to the Scotian Shelf. *Pseudocalanus minutus* was frequent during all cruises, with all copepodite stages evident in the summer. *Sagitta elegans* has a reproducing population in St. Margaret's Bay (Sameoto 1971). The status of *C. hyperboreus*, *C. glacialis*, and *M. longa* is less clear. The first two species are common on Emerald Bank in May and June but are virtually absent after July. Whether they maintain a breeding population in the northeast of the Scotian Shelf is unknown.

TABLE 3. Summary of recurrent groups of zooplankton on the Scotian Shelf during eight cruises from August 1978 to September 1980 showing number of cruises during which any pair of taxa had an index of affinity ≥ +0.5.

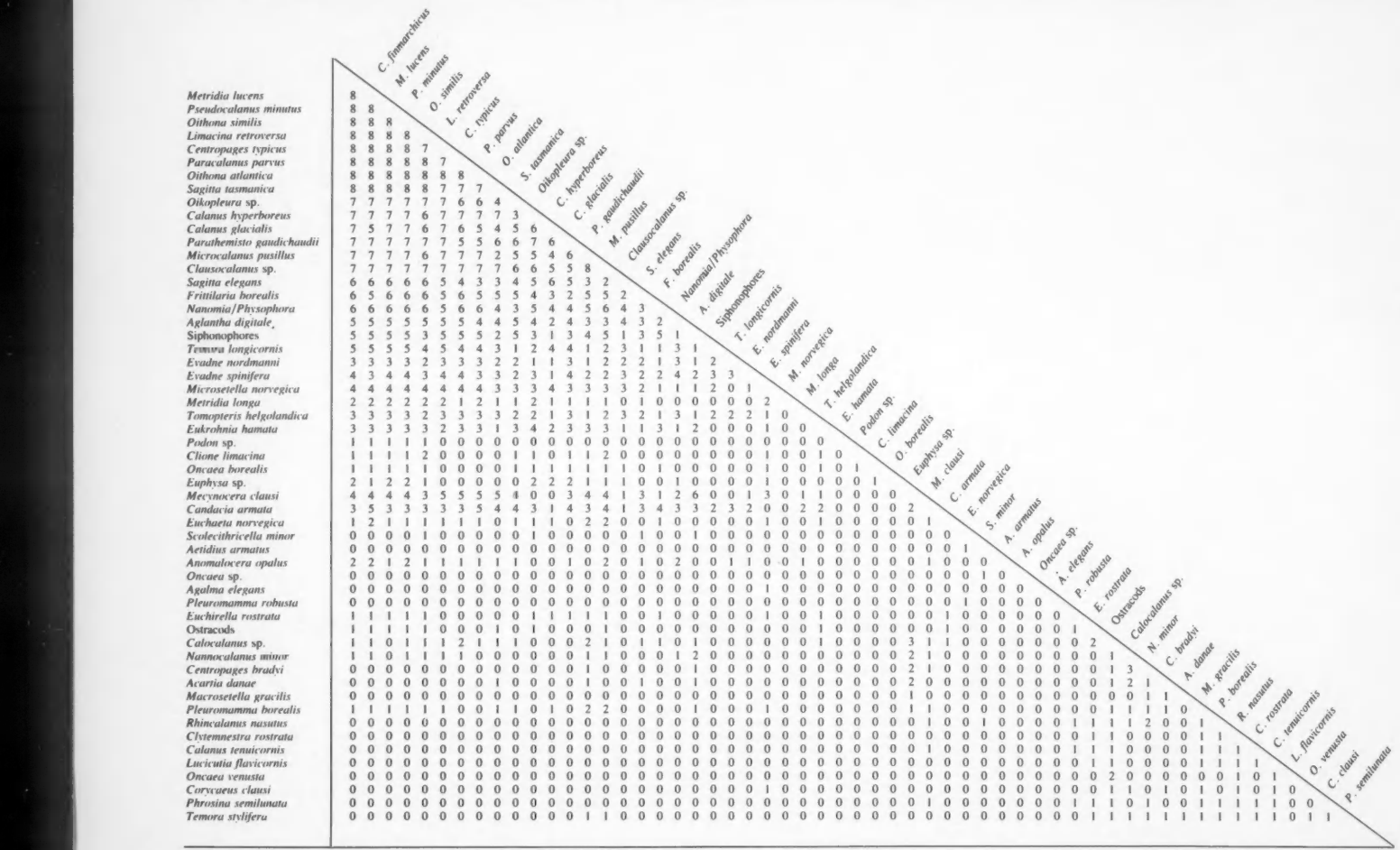


TABLE 4. August 1978 cruise. Species scores on RA axis one and correlations ($*P < 0.05$) of abundance codes with station scores, station $n = 39$.

Species/taxon	Score on RA axis one	Spearman rank correlation
Pleuromamma abdominalis	0.0	−0.38*
Phronima sedentaria	0.0	−0.38*
Clytemnestra rostrata	4.7	−0.44*
Lucicutia flavicornis	4.7	−0.44*
Calanus tenuicornis	5.2	−0.53*
Rhincalanus nasutus	5.2	−0.53*
Phrosina semilunata	5.2	−0.53*
Calocalanus sp.	6.9	−0.44*
Pleuromamma borealis	10.5	−0.63*
Temora stylifera	11.2	−0.58*
Candacia armata	13.8	−0.51*
Corycaeus clausi	19.0	−0.53*
Scolecithrix danae	21.0	−0.34*
Oncaea venusta	23.8	−0.31
Ostracods	24.2	−0.47*
Nannocalanus minor	24.7	−0.73*
Pleuromamma robusta	27.2	−0.32*
Centropages bradyi	28.2	−0.66*
Scolecithricella minor	28.4	−0.40*
Sagitta enflata	28.4	−0.42*
Clausocalanus sp.	29.4	−0.67*
Acartia danae	32.8	−0.74*
Clio pyramidata	42.1	−0.32*
Microcalanus pusillus	42.6	−0.76*
Siphonophores	44.2	−0.66*
Euchirella rostrata	49.5	−0.37*
Mecynocera clausi	53.0	−0.74*
Thaliacea	54.5	−0.44*
Macrosetella gracilis	55.5	−0.48*
Euchaeta norvegica	60.6	−0.23
Sagitta tasmanica	69.6	−0.49*
Fritillaria borealis	73.1	−0.27
Metridia lucens	74.8	−0.04
Anomalocera opalus	75.4	−0.04
Oikopleura sp.	76.4	−0.34*
Microsetella norvegica	78.3	−0.07
Oithona atlantica	78.4	−0.05
Oithona similis	80.4	0.24
Limacina retroversa	81.3	0.30
Metridia longa	82.2	0.29
Aglantha digitale	85.1	0.19
Paracalanus parvus	85.2	0.14
Pseudocalanus minutus	86.2	0.67*
Calanus finmarchicus	86.8	0.60*
Parathemisto gaudichaudii	87.2	0.37*
Evadne nordmanni	88.3	0.36*
Sagitta elegans	88.5	0.68*
Centropages typicus	90.3	0.49*
Evadne spinifera	90.6	0.31
Calanus hyperboreus	92.2	0.49*
Nanomia/Physophora	92.8	0.01
Calanus glacialis	93.1	0.44*
Tomopteris helgolandica	93.5	0.22
Hyperia galba	95.4	−0.32*
Temora longicornis	95.4	0.73*
Podon sp.	96.2	0.41*
Tortanus discaudatus	100.0	0.28

TABLE 5. January–February 1979 cruise. Species scores on RA axis one and correlations ($*P < 0.05$) of abundance codes with station scores, station $n = 24$.

Species/taxon	Score on RA axis one	Spearman rank correlation
Temora longicornis	0.0	−0.45*
Sagitta elegans	7.7	−0.63*
Metridia longa	22.3	−0.45*
Calanus hyperboreus	25.0	−0.54*
Euphysa sp.	26.9	−0.32
Euchaeta norvegica	27.9	−0.40
Pleuromamma robusta	29.4	−0.33
Tomopteris helgolandica	43.7	−0.23
Candacia armata	47.1	−0.33
Calanus glacialis	47.2	−0.56*
Parathemisto gaudichaudii	53.4	−0.18
Metridia lucens	54.5	−0.50
Ostracods	55.0	−0.21
Pleuromamma borealis	56.1	−0.33
Pseudocalanus minutus	57.1	−0.65*
Oncaea sp.	57.9	−0.14
Microsetella norvegica	58.2	−0.30
Oikopleura sp.	59.0	−0.38
Sagitta tasmanica	59.1	−0.20
Calanus finmarchicus	59.5	−0.37
Fritillaria borealis	60.7	−0.14
Centropages typicus	60.9	−0.20
Oithona similis	63.4	0.00
Clausocalanus sp.	64.8	−0.13
Microcalanus pusillus	65.7	−0.18
Limacina retroversa	65.9	0.04
Nanomia/Physophora	67.6	0.10
Oithona atlantica	69.6	0.20
Paracalanus parvus	73.7	0.17
Mecynocera clausi	78.1	0.19
Siphonophores	78.6	0.48*
Nannocalanus minor	91.9	0.35
Scolecithricella minor	94.8	0.28
Agalma elegans	100.0	0.45*

INTERMEDIATE TAXA

These include most of the core recurrent group (those species having positive indices of affinity in all cruises): *C. finmarchicus*, *M. lucens*, *O. similis*, and *L. retroversa* (Table 3). Together with *Centropages typicus*, the above three copepods comprise the dominant fraction of the zooplankton and approximately 80% of the annual copepod production on Emerald Bank (Tremblay and Roff 1983). Most of the intermediate species in Fig. 3 have been classified as boreal (Fish and Johnson 1937) or northern intermediate (Colebrook 1964).

All the intermediate taxa are indigenous to the Scotian Shelf. This is evident from the regular occurrence of early copepodite stages of *C. typicus*, *C. finmarchicus*, *O. similis*, and *M. lucens*.

OFFSHORE TAXA

Most of the offshore species in Fig. 3 were found farther offshore by Sameoto and Lewis (1980a, 1980b) and have been classified as oceanic by several workers. Colton et al.

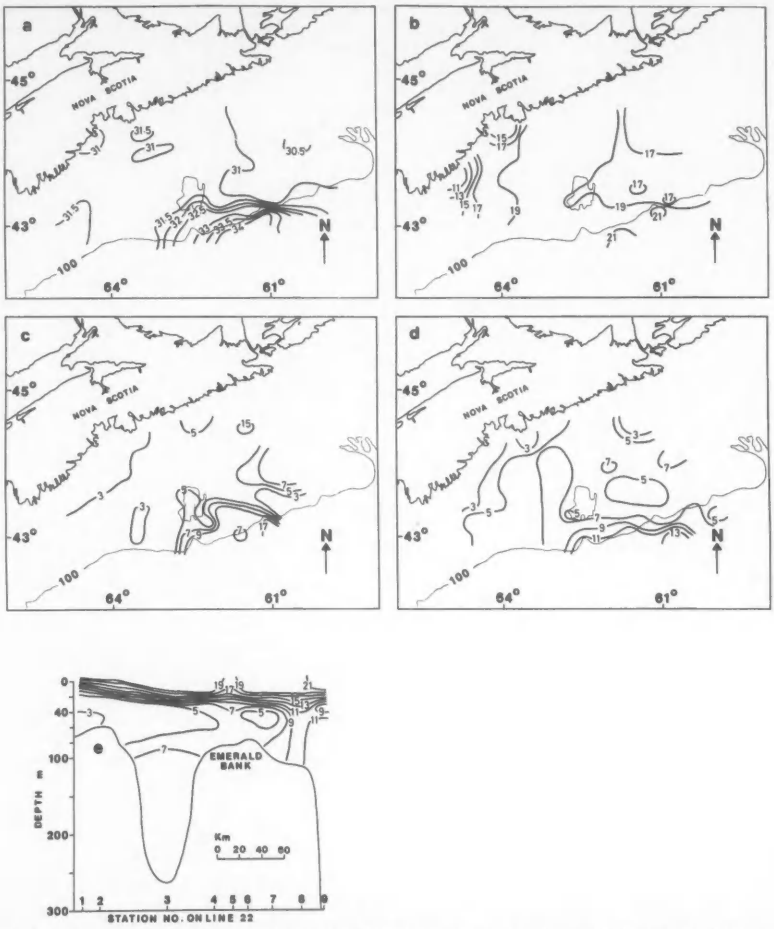


FIG. 6. Hydrographic features on the Scotian Shelf and upper slope in August 1978 (contoured from 66 observations). (a) Surface salinity (parts per thousand); (b) surface temperature (degrees Celsius); (c) temperature at 50 m or bottom; (d) temperature at 100 m or bottom; (e) temperature profile through Emerald Bank. Depth contour is in fathoms (1 fathom = 1.85 m).

(1962) used several of the offshore species in Fig. 3 as indicators of the encroachment of southern oceanic waters in the Gulf of Maine and Georges Bank, e.g. *Mecynocera clausi*, *Rhincalanus nasutus*, and *P. borealis*. Although most offshore species were of southern origin, *Euchaeta norvegica* and *Scolecithricella minor* are northern oceanics (Bigelow 1926; Colebrook 1972; Cox and Wiebe 1979), as may be the case for *M. pusillus*.

Paracalanus parvus, although ranked as an offshore species, was representative of a small number of species which had seasonally dependent ecological status. This copepod tends to be associated with the warmer part of the Scotian Shelf in winter and spring but is distributed evenly or is more abundant in the cooler parts of the shelf in summer and fall.

The very sporadic occurrences of most offshore species on the shelf indicates that they can be further classified as expatriates; several are exotic expatriates, dying soon after encountering shelf waters. The 10 species scored lowest in Table 4 are good examples; if they occurred on the shelf at all it was usually as adults. Others may survive on the shelf to varying degrees. The occurrence of spermatophores on *C. armata* females from the Emerald Bank in two cruises in late summer 1980, coupled with observations of early copepodite stages, indicates that this species was reproducing on the Scotian Shelf. Its absence during most of the year, however, indicates that it does not maintain a viable population there. *Clausocalanus* sp. was at times frequent over much of the shelf but was most abundant on the outer edge. Its almost

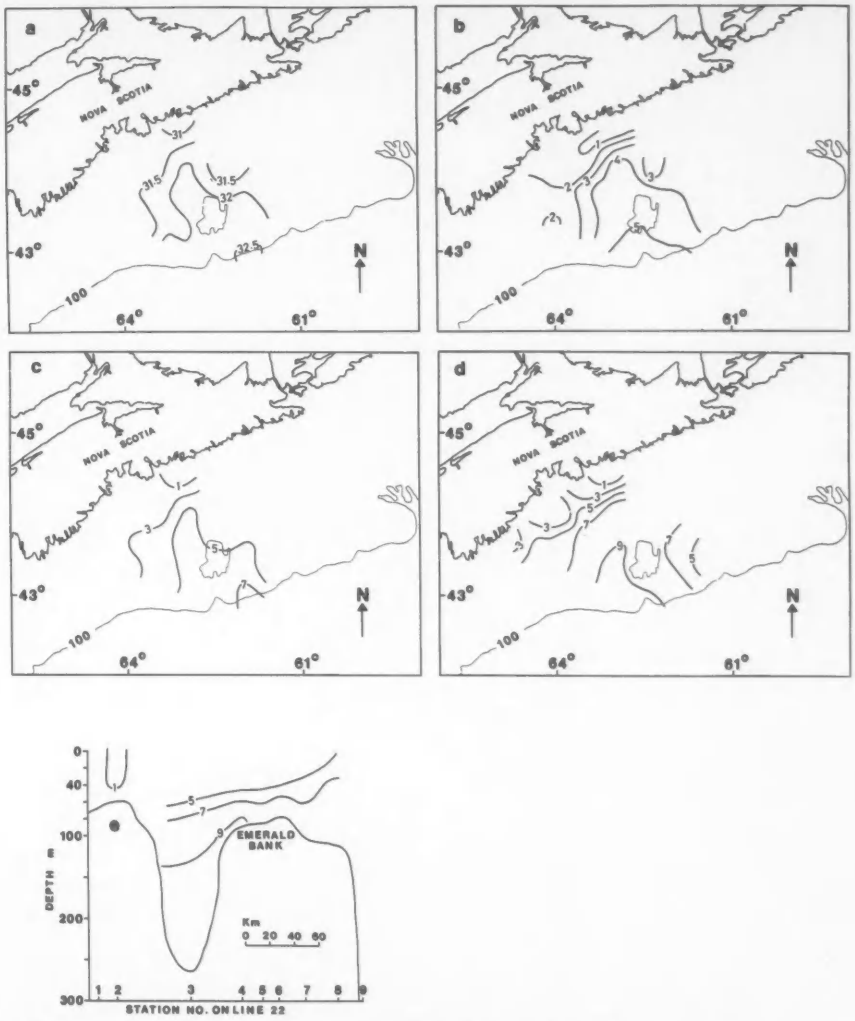


FIG. 7. Hydrographic features on the Scotian Shelf and upper slope in January–February 1979 (contoured from 36 observations). (a) Surface salinity (parts per thousand); (b) surface temperature (degrees Celsius); (c) temperature at 50 m or bottom; (d) temperature at 100 m or bottom; (e) temperature profile through Emerald Bank. Depth contour is in fathoms (1 fathom = 1.85 m).

complete absence at shelf stations in August 1978, and the fact that Willey (1919) never found it on the shelf, is evidence that it does not maintain a permanent population there.

Thus, survival of offshore species of invertebrate zooplankton on the Scotian Shelf is similar to other groups. Markle et al. (1980) stated: "Warm water fishes there range from the lottery larvae dispersed by the Gulf Stream, to the species that can survive temporarily, to species which appear to be able to complete their life cycle within its confines."

The lack of a consistent seasonal trend in the strength of the inshore–offshore community gradient indicates that variability was related to aperiodic hydrographic events. Probably the most important of these are incursions of slope water, which have been observed numerous times on the Scotian Shelf (Hachey 1937, 1953; McLellan et al. 1953; Fournier et al. 1979). Although Gulf Stream rings impinging on the Continental Shelf are known to be of significance farther south (Saunders 1971; Lai and Richardson 1977; Cox and

Wiebe 1979) their importance to the Scotian Shelf hydrography has not been evaluated.

The retrograde subsurface front observed in January–February 1979 (Fig. 7e) is very similar to that documented by Hachey (1953) and indicates an incursion of deeper slope water. Fournier et al. (1979) documented a more intense, almost horizontal subsurface front in March of another year, but little is known about the frequency or the symmetry of such incursions.

Slope water intruding at the surface and at intermediate depths can cause faunal mixing in the horizontal plane and thus diminish inshore–offshore differences. Alternatively, if the slope water is intruding only at greater depths, it can cause the zooplankton gradient to be shifted towards the vertical plane. Unless discrete depth intervals are sampled, this shift will appear simply as horizontal mixing. In January–February 1979 only one of the offshore taxa was shown to be more abundant in deeper waters. It is possible that offshore taxa gain access to the shelf via deeper waters and then migrate into the upper layers. Sporadic intrusions of deeper waters, and the consistent presence of warm high-salinity water in the deeper layers of the Scotian Gulf, suggest that the vertical aspect of the inshore–offshore gradient is important to the zooplankton community on the Scotian Shelf.

The inshore–offshore community gradient is strongly correlated with an environmental gradient. Although a consistent feature, the environmental gradient is periodically altered by incursions of slope water, which in turn affect the community gradient. A less prevalent east–west community gradient is no doubt affected by changes in the volume of water flowing from the northeast. Given this predominantly advective environment, or ecotone, zooplankton community structure on the Scotian Shelf appears to be determined primarily by species–environment relationships rather than species–species relationships as in the central oceanic gyres (McGowan and Walker 1979).

Strong biological relationships imply coevolution, which in turn implies a long period of sharing the same environment in a predictable manner. This seems unlikely for many of the species which converge on the shelf, given the apparent aperiodic nature of events such as slope water incursions.

Advective processes are also important in a consideration of trophodynamics. The net effect of slope water incursions on the Scotian Shelf is unclear, since they may not affect different trophic levels in the same manner. Advections of nutrient-rich slope water can enhance primary production both directly (Fournier et al. 1977) and indirectly by decreasing the mixed layer depth (Fournier et al. 1979). Such incursions may thus represent an energy supplement which should result in increased zooplankton production. Also, indigenous larval fish can capitalize on expatriate zooplankton species as food items (L. J. Coates-Markle and J. C. Roff unpublished data). Conversely, an energy loss could result from slope water incursions, and temporary exploitation by offshore predators (such as salps or the copepod *C. armata*) could have an impact on local populations (Cox and Wiebe 1979).

Now that gradients can be defined, further understanding of zooplankton community structure and trophodynamics on the Scotian Shelf hinges on increased knowledge of horizontal and vertical distributions in relation to hydrographic features (e.g. Herman et al. 1981; Sameoto 1982) and of the reactions of inshore, intermediate, and offshore zooplankton to specific hydrographic events.

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Predicting Natural Mortality Rates and Reproduction–Mortality Trade-offs from Fish Life History Data

R. A. MYERS AND R. W. DOYLE

Department of Biology, Dalhousie University, Halifax, N.S., B3H 4J1

MYERS, R. A., AND R. W. DOYLE. 1983. Predicting natural mortality rates and reproduction–mortality trade-offs from life history data. Can. J. Fish. Aquat. Sci. 40: 612–620.

A method for estimating natural mortality and evolutionary constraint on fish life histories is presented based on the assumption that observed life histories are evolutionarily stable. Inverse optimization techniques are used to determine the values of natural mortality, reproduction–mortality trade-offs, and energy conversion efficiencies that would make observed life histories evolutionarily stable. The life history method yields natural mortality estimates comparable with those based on population age–frequency data. Sensitivity analysis is used to determine the robustness of the predictions to errors in parameter estimation and density-dependent factors.

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Nous présentons ici une méthode pour estimer la mortalité naturelle et les contraintes évolutionnaires sur le cycle de vie des poissons. Cette méthode repose sur l'hypothèse que les cycles de vie observés sont stables sous le rapport de l'évolution. Des techniques d'optimisation inverse ont été utilisées pour déterminer la mortalité naturelle, les compromis reproduction–mortalité et les rendements énergétiques susceptibles de stabiliser les cycles de vie observés. La méthode donne des estimations de mortalité naturelle comparables à celles que donnent les fréquences d'âge d'une population. Nous faisons appel à une analyse de sensibilité afin de déterminer la solidité des prédictions face aux erreurs d'estimations de paramètres et aux facteurs qu'influence la densité.

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MOST estimates of the rate of natural mortality in fish populations have been derived from age–frequency data or by mark–recapture methods. Both of these methods are very sensitive to biases in sampling technique. They also lead to estimates with large standard errors for all but the largest sample sizes. The biases and standard errors are large and somewhat unreliable because many parameters (age-specific natural and fishing mortality rates, immigration and emigration rates, etc.) must be estimated from the same body of data on catch rates of fish at different ages. Despite their unreliability, estimates of natural mortality are important parameters in analytical techniques designed to assess stock sizes, including various types of cohort analysis (Ricker 1975).

It would clearly be desirable to be able to check some of these estimates using data of an entirely different kind, if the data were available and appropriate analytical techniques could be developed. In this paper we attempt to use life history information about fish populations to make estimates of natural mortality rates.

The analytical technique that we use to relate the life history to the population dynamics is based on the assumption that fish life histories are evolutionarily stable (Maynard Smith 1974). A population is evolutionarily stable, with respect to a phenotype or set of phenotypes, if a rare gene introduced into the population will always be eliminated if its carriers have a phenotype different from the population mean (Charlesworth 1980, p. 231). Using techniques based on this assumption, it is possible to estimate natural mortality, identify possible constraints on growth and reproduction, and determine whether estimates of population and life history parameters are internally consistent. In our analysis, the age-specific natural mortality rates are considered to be the environmentally determined rates to which the population is adapted in such a way that the life history is evolutionarily stable. We shall term our estimate of natural mortality the best adapted (BA) estimator.

By evolutionary constraints we mean the limitations on the range of possible phenotypes or modes of adaptation. This range will, in turn, impose limits on natural selection (at least

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in the short term or within the set of genotypes/phenotypes which can be considered a single species). We shall, in particular, be concerned with two constraints: (1) the additional probability of mortality a fish incurs because of the energy it invests in reproduction and (2) the conversion efficiency of energy into eggs relative to the conversion efficiency into somatic material. When one examines fish life histories in terms of optimality or lack of it, one feature appears overwhelmingly important: most fish continue to grow after they reach sexual maturity. As it turns out, postmaturational growth is evolutionarily stable only under restrictive conditions.

An implicit assumption in our analysis is that the data we use on growth rates, fecundities, ages-at-maturity, etc., relate to a mortality rate which has some "real-world" relevance. If there have been no significant phenotypic or genetic changes in the fish communities due to exploitation, the BA estimator should estimate the primordial mortality rate. However, fish stocks that have been heavily fished for many decades may no longer have their original life histories (Borisov 1978; see Doyle and Myers 1982 and Doyle 1983 for methods of estimating the selection intensity in natural populations). To the extent that these new life histories are not yet evolutionarily stable, the estimated mortality rates and evolutionary constraints will be biased away from both primordial and current values. Whether these biases are serious remains to be seen.

Formulation of the Model

We shall use data on female fish, but the approach can also be applied to males. We shall assume that the effects of selection on males via genetic correlations between the sexes is insignificant (Falconer 1960; Lande 1980). We shall consider a population censused at the beginning of the breeding season. All individuals will fall into age classes $1,2,\ldots,T$. We shall write l_x as the probability of a female surviving from fertilization to the beginning of the breeding season when she is of age x. The expected number of female zygotes produced at age x will be m_x. For the density-independent case, the evolutionarily stable life history will correspond to the l_x' survivorship schedule and m_x' fecundity schedule that yield a local maximum in the intrinsic rate of natural increase, r', which is given by the discrete-time version of Lotka's equation (Taylor et al. 1974; Charlesworth 1980, p. 232). That is, for any other survivorship and reproduction schedule, l_x^* and m_x^* (Charlesworth and León 1976)

$$(1) \quad \sum_{x=1}^{T} \exp(-r'x) l_x^* m_x^* < \sum_{x=1}^{T} \exp(-r'x) l_x' m_x' = 1.$$

The reproductive schedules will be calculated as follows. The change in weight of a female over 1 yr can be described by

$$(2) \quad w_{x+1} = w_x + (1 - u_x) f(w_x)$$

where $f(w_x)$ is the energy available for growth and reproduction for a fish of weight w and u_x is the proportion of that energy that goes into reproduction at age x. The function $f(w_x)$ is the net energy discounted for standard metabolism and locomotion, i.e. the surplus energy (Ware 1980). If population density effects are ignored, one form of the surplus energy is

$$(3) \quad f(w_x) = \alpha w_x^{\beta}.$$

If the relationship between surplus energy and weight differs greatly for young and old fish, the above allometric relationship may not be adequate to describe the entire life cycle, as assumed in this analysis.

The expected number of female zygotes produced by a female aged x is

$$(4) \quad m_{x+1} = g(u_x) f(w_x),$$

where $g(u_x)$ is the conversion function of energy into female zygotes (female zygotes will be referred to as "eggs"). That is, $g(u_x)/u_x$ is the conversion efficiency of energy into eggs. For an intrinsic rate of increase, r, the problem of finding the evolutionarily stable life history reduces to the maximization problem:

$$(5) \quad \max_{u_1,\ldots,u_{T-1}} \sum_{x=2}^{T} \exp(-rx) l_x m_x(w_{x-1}, u_{x-1}).$$

The above model cannot produce an evolutionarily stable life history with postmaturational growth if $g(u_x)$ is linear (Taylor et al. 1974).

The general question of what kinds of constraints are sufficient, and are not sufficient, to make postmaturational growth evolutionarily stable can be investigated by using control theoretic methods (Taylor et al. 1974; León 1976). Constraints and environmental factors that are in general not sufficient to make postmaturational growth evolutionarily stable are (R. A. Myers, unpublished results) (1) weight-dependent mortality, (2) surplus energy functions that have a more complex dependence on weight than eq 3, (3) the inclusion of two control variables (energy allocated to maintenance, as well as growth versus reproduction), (4) density dependence, (5) stochastic surplus energy functions, and (6) stochastic mortalities.

There are two specific constraints on phenotypes that can, however, produce postmaturational growth. We shall consider these two constraints in some detail. Postmaturational growth is evolutionarily stable if the energy cost per egg increases as the amount of energy devoted to reproduction increases (the "concave energy conversion" constraint) (Taylor et al. 1974). Postmaturational growth will also be evolutionarily stable if mortality associated with reproduction increases as a convex function of the proportion of energy devoted to reproduction (the "convex mortality" constraint). A function, f, is convex if for any pair of points on the graph of f the line segment joining these two points lies above or on the graph of f, and similarly for a concave function.

Relatively precise estimates can be made of the magnitude and functional form of the above relationships required for an observed fish life history to be evolutionarily stable. This estimation procedure produces useful numerical predictions of population parameters, e.g. natural mortality rates. However, it is impossible to distinguish between these two

alternate constraints on a purely theoretical basis or with the data that are currently available. Both mechanisms could be acting together to produce the observed life histories. Here, the assumption is that postmaturational growth is due to one or both constraints.

Biological Basis of the Constraints

Mechanisms Leading to Concave Egg Conversion Function

There are a number of phenomena that could produce a concave egg conversion function in fish. Among these are the following:

1) Limitations of space for carrying eggs. If the number of eggs a fish can produce is more than the number it can carry, this will constrain the amount of energy that can be efficiently expended on reproduction at any age (Hubbs et al. 1968). This constraint is circumvented by the practice, characteristic of some species, of ripening batches of eggs sequentially (Hunter and Goldberg 1980). There may, however, be selective pressures for synchronous reproduction, as there appears to be on plants (Janzen 1976), or there may be a relatively short season in which offspring survival is best (Cushing 1975). Either may create concave egg conversion functions.
2) Nutrient limitation on egg production. If there are essential nutrients that are either not available or are energetically expensive for a fish to obtain, a concave egg conversion function could result. In the common sole, *Solea vulgaris*, final oocyte maturation appears to depend on essential amino acids not found in all foods (Fluechter and Trommsdorf 1974).
3) Some fishes develop their eggs almost exclusively on stored reserves, e.g. the American plaice (*Hippoglossoides platessoides*) (MacKinnon 1972). If there is an energy cost to storing this energy reserve (which increases as a convex function of the amount of energy stored), or if only a limited amount of energy can be stored, a concave egg conversion function could result.
4) Indirect energetic cost due to egg production. There may be energetic costs to egg production beyond those required to produce eggs. If these energetic costs increase as a convex function of the proportion of surplus energy allocated to reproduction, then a concave egg conversion function will result. Also, the energetic costs of protecting or carrying eggs or young may increase disproportionately as the number of eggs or young increase.
5) Decreased food intake is associated with reproduction in some fish species. An extreme case are those species of mouth brooders that do not eat during reproduction (Fryer and Iles 1972). In this case, eq 4 is an oversimplification and must be replaced by

$$m_{x+1} = g(u_x)f(w_x, u_x)$$

where $f(w_x, u_x)$ is now a decreasing function of u_x. If the whole quantity $g(u_x)f(w_x, u_x)$ is a concave function of u_x, postmaturational growth can occur. We know of no attempt to quantify the loss of feeding due to reproduction, as done for lizards (Shine 1980). In our calculations below, we assume that eq 4 is an adequate description of reproduction. For species in which it is not an adequate description, the decrease in surplus energy due to reproduction must be determined experimentally before our methods can be used.

Mechanisms 3, 4, and 5 could pose problems in analyzing published data, since the surplus energy as measured by the summation of gonad energy content and incremental weight increase (Ware 1980) would underestimate surplus energy.

Mechanisms Leading to Convex Reproduction Mortality Trade-offs

A number of phenomena may lead to reproduction–mortality trade-offs. Examples include the following.

1) Greater predation accompanying reproduction. Egg production is often associated with a loss of muscle tissue (Shevchenko 1972). This may reduce locomotory capabilities and lead to increased predation.
2) Increased susceptibility to disease has been suggested as a cause of reproduction–mortality trade-off (Orton 1929).

Either prereproduction or postreproduction mortality can (if it is a convex function of u_x) lead to the evolutionary stability of postmaturational growth. Here, we shall consider only prereproduction mortality.

There is, unfortunately, no evidence to suggest what shape the curve of mortality as a function of the proportion of surplus energy allocated to reproduction might take. In particular, it is not known whether mortality is a convex function of energy allocated to reproduction. Some types of reproduction–mortality may not be a convex function of u_x, e.g. the mortality incurred during a spawning migration.

Methods

We made two estimates of natural mortality for each stock studied. First, we assumed that postmaturational growth was due to a convex reproduction–mortality trade-off (and the egg conversion function was linear). Second, we assumed that postmaturational growth was due to a concave egg conversion function (and that there was no reproduction–mortality trade-off). The result is two estimates of natural mortality, each based on one of the above assumptions.

Several types of data are required in the analysis. These are (1) growth rate over the natural life span of the species, (2) fecundity estimates over the life span of the species (weight fecundity data may sometimes be used), (3) estimates of energy content of eggs, and (4) estimates of age and size at sexual maturity. Species chosen for the analysis were those for which the above could be estimated with reasonable accuracy.

Several surplus energy estimates that we used came from Ware (1980). When making estimates it is important to state the range of ages over which the estimates are made. For example, an allometric relationship gave an adequate fit for the surplus energy for American plaice from age 6 only. The surplus energy estimates for North Sea plaice (*Pleuronectes platessa*), perch (*Perca fluviatilis*), and whitefish (*Coregonus clupeaformis*) were calculated over ages 1 to T.

The maximum life span is difficult to estimate for long-lived fish from heavily exploited stocks because few individuals reach senescence. For those populations from which no estimates are available, we estimated the maximum age as the age at which a fish reaches 97% of its asymptotic length, based on published von Bertalanffy growth curves. The estimates of T from the growth curves were consistent with the estimates of the maximum recorded age.

The functional form that was assumed for the reproduction–mortality trade-off constraint was

$$(6) \quad Q_x = Q_a + C_1 u_x^{\gamma_1}$$

where Q_x is the probability of dying from age x to $x + 1$, Q_a is the mortality if there is no reproduction, C_1 is the mortality if all surplus energy is channeled into reproduction, and γ_1 is a power term used to describe the nonlinearity of the response (Fig. 1). Using the above notation:

$$(7) \quad l_x = \prod_{y=1}^{x-1} (1 - Q_y).$$

The standard fisheries notation for instantaneous natural mortality, M (Ricker 1975), is written as

$$(8) \quad \exp(-M) = 1 - Q_x.$$

The egg conversion function is

$$(9) \quad g(u_x) = u_x - C_2 u_x^{\gamma_2}$$

where C_2 is the reduction in viable eggs or offspring at maximum u_x and γ_2 is a power term (Fig. 2). The mortality under the assumption of concave egg conversion function is Q_b. We shall assume that the intrinsic rate of increase is approximately equal to zero for our estimates of natural mortality.

The estimation procedure for natural mortality, the egg conversion function parameters, and the reproduction–mortality trade-off parameters used were as follows. The parameters of the egg conversion function and the reproduction–mortality constraints (eq 6 and 9) along with natural mortality were estimated by iteration such that the age (or weight) at sexual maturation, the final weight, and the values of u_x were as close as possible to the observed values. The iterative procedure used to determine Q_a, Q_b, C_1, C_2, γ_1, and γ_2 was as follows.

1) The α and β surplus energy parameters (eq 3) were determined as in Ware (1980).
2) The observed life history of the population was obtained, e.g. age and weight at sexual maturation (see Table 1 for the data sources).
3) The evolutionarily stable life history (eq 5 modified by eq 6 or 9) was determined for an observed α and β for a trial Q_a, C_1, γ_1 or Q_b, C_2, γ_2. The predicted life history under the trial natural mortality and life history constraints was compared with the observed life history obtained in step 2.
4) New trial natural mortality and life history constraints were selected and step 3 was repeated systematically until the evolutionarily stable life history from a trial matched the observed life history.

The determination of the evolutionarily stable life history for a trial set of natural mortality and life history constraints was determined by a dynamic programing algorithm (Bellman 1957). The difference between the observed and the trial life history is minimized by matching the weight at maturity, asymptotic weight, and the shape of the plot of u_x versus x. The sensitivity of the estimates to incorrect parameter estimation is discussed below.

Results

The results of the analysis of several fish stocks are summarized in Table 1. Two BA estimates of natural mortality are made: (1) Q_a given by eq 6, which is the estimate obtained under the assumption that postmaturational growth is due to a reproduction–mortality trade-off (age-specific mortality can be estimated from eq 6) and (2) Q_b, which is the estimate under the assumption that postmaturational growth is due to a concave energy conversion function. Table 1 contains observed data (e.g. weight at maturity) calculated surplus energy parameters (α and β), estimates of natural mortality obtained from the literature, BA estimates of natural mortality, and estimates of the evolutionary constraints (C_1, C_2, γ_1, and γ_2).

The relatively small amount of postmaturational growth in herring implies a small reproduction–mortality trade-off (Fig. 1) or a relatively linear egg conversion function (Fig. 2). When the transition from the total surplus energy being devoted to growth to the majority of surplus energy being devoted to reproduction is spread over many age classes as in Atlantic cod (*Gadus morhua*), rather than a few as in Atlantic herring (*Clupea harengus*) (Ware 1980), the predicted egg conversion functions and reproduction–mortality trade-offs are quite different. The transition is gradual because the egg conversion function is more concave and the reproduction–mortality trade-off is more convex. The opposite occurs if the transition period is short. There are considerable differences among the estimates of natural mortality, egg conversion functions, and reproduction–mortality trade-offs for cod of different stocks.

Estimates of mortality are similar under the assumption of a concave conversion function with no reproduction–mortality trade-off or under the assumption of a reproduction–mortality trade-off with a linear egg conversion of efficiency, and the natural mortality rates that make the observed life histories evolutionarily stable are almost identical under either assumption (Table 1).

Natural mortality estimates obtained from the literature are compared with the BA estimator in Fig. 3. The two estimates are generally very similar. Note that the estimate of natural mortality for Atlantic cod from the Gulf of St. Lawrence deviates greatly from published estimates. If the estimates of surplus energy given by Ware (1980) are correct, then the high published estimates of natural mortality are inconsistent with the hypothesis that this stock is adapted to its environment. We suggest that the published estimates of natural mortality are too high or the estimates of growth rates (or fecundity) are too low.

TABLE 1. The observed life history traits and predicted natural mortalities, reproductive mortality trade-offs, and egg conversion functions for several fish populations. The surplus energy parameters are α and β, W_M and W_∞ are the weight at sexual maturation and asymptotic weight, and T is the maximum assumed life span. The predicted natural mortality if no reproduction occurs is Q_a under the assumption that postmaturational growth is due to a reproduction mortality trade-off, predicted natural mortality is Q_b under the assumption that postmaturational growth is due to a concave conversion function, and the predicted reproductive mortality trade-off is described by the two parameters, C_1 and γ_1, where C_1 is the maximum mortality due to reproduction and γ_1 is an allometric constant (see eq 6). The predicted egg conversion functions are described by C_2, the reduction of the egg conversion function at $u_s = 1$, and γ_2, an allometric constant (see eq 9). The instantaneous natural mortalities obtained from the literature, M_T, are compared with BA estimators, M_{BA} (from the value of Q_b). Mortality was estimated via traditional methods using combined data for males and females (except for American plaice). Accurate traditional estimates of natural mortality rates of South Gulf herring and mackerel were unavailable.

Stock	α	β	W_M(g)	W_∞(g)	T(yr)	Q_a	C_1	γ_1	Q_b	C_2	γ_2	M_T	M_{BA}	Source[b]
Atlantic cod (*Gadus morhua*)														
Southern Gulf[a]	7.7	0.59	1250	25 000	35	0.08	0.21	2.5	0.07	0.6	1.8	0.15[c]	0.07	1, 11
North Sea	40	0.51	2000	14 400	14	0.21	0.09	2.5	0.20	0.4	2.5	0.20	0.22	4, 11
Grand Banks	12	0.59	1200	23 000	30	0.15	0.15	1.8	0.15	0.5	1.7	0.2	0.16	2, 11
Atlantic herring (*Clupea harengus*)														
Southern Gulf[a]	0.46	0.96	190	290	19	0.26	0.007	5	0.26	0.035	4	—	0.3	11
Dogger Bank	0.26	1.09	120	200	12	0.29	0.05	4.5	0.29	0.1	2.5	0.25	0.34	1, 11
Atlantic mackerel (*Scomber scombrus*)														
Southern Gulf[a]	0.46	0.98	220	1070	14	0.13	0.2	3	0.13	0.4	3.5	—	0.14	11
American plaice (*Hippoglossoides platessoides*)														
Grand Banks	0.08	1.10	1400[d]	2970[d]	25	0.11	0.06	3.4	0.11	0.3	2	0.13	0.12	6, 7
Plaice (*Pleuronectes platessa*)														
North Sea	5.7	0.56	200	2870	22	0.9	0.12[c]	3	0.1	0.45	2.5	0.12	0.11	3, 8
Perch (*Perca fluviatilis*)														
Windermere Lake	0.89	0.95	50	400	14	0.38	0.09	2.5	0.37	0.29	1.7	0.39	0.46	10
Whitefish (*Coregonus clupeaformis*)														
Shakespeare Island	10.8	0.46	350	16 000	27	0.11	0.06	4	0.11	0.25	4	0.13	0.12	5, 9

[a]Southern Gulf of St. Lawrence (4*T*).

[b]Sources: 1, Beverton 1963; 2, Beverton 1965; 3, Beverton and Holt 1957; 4, Beverton and Holt 1959; 5, Healey 1975; 6, Pitt 1975; 7, Powles 1969; 8, Simpson 1951; 9, Ricker 1946; 10, Thorpe 1977; 11, Ware 1980.

[c]Traditional estimate of mortality for southern Gulf of St. Lawrence cod midpoint range given by Beverton (1963). Dickie (1963) estimated higher rates from tagging studies.

[d]Gutted weight.

Limitations and Sensitivity Analysis

LIMITATIONS OF THE ACCURACY OF THE METHOD

The methods we have used are dependent on the accurate calculation of the surplus energy function. If there are significant indirect costs to egg production that are not included in the calculations of surplus energy (e.g. extra energy required for brooding eggs), the natural mortalities will be underestimated. Also, the parameters C_1 (eq 6) and C_2 (eq 9) of the reproduction–mortality trade-off and egg conversion function will be overestimated.

We made no attempt to include a decrease in surplus energy late in life due to senescence (Woodhead 1979). We assumed that so few fish reach the age of senescence, because of predation and disease, that it was not necessary to allow for a late decrease in surplus energy. The relative insensitivity of the estimates to changes in the maximum age (Table 2) suggests that this assumption is reasonable. In general, genes affecting life history traits expressed earlier in life will be selected for more strongly than those expressed later (Charlesworth 1980, p. 206).

We have assumed that the reproduction–mortality function and the egg conversion function do not vary with age or weight. While these assumptions may not always be valid, there are currently insufficient data to extend the model to include these factors.

SENSITIVITY ANALYSIS

Sensitivity analysis (Tomovic 1963) was employed to determine the relative importance of misspecification of the biological variables in the model to the predicted evolutionarily stable solution. The technique employed was as follows.

1) Each of the system parameters (e.g. the surplus energy parameters) was varied and the resulting evolutionarily stable changes in the natural mortalities, reproduction–mortality trade-off, and egg conversion functions were determined.
2) Estimates of the partial derivatives of the changes in the predicted natural mortalities, reproduction–mortalities, and concave conversion functions were made (Table 2, unnormalized) by differentiation of a polynomial fit to the results obtained in 1.

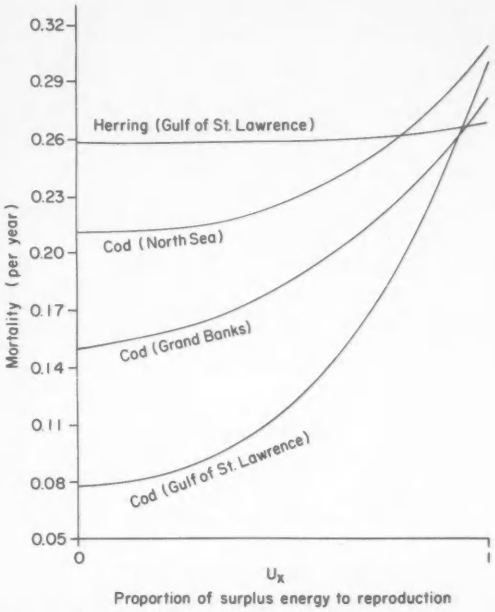

FIG. 1. Predicted natural mortality due to reproduction required to make the observed life histories evolutionarily stable. This reproductive mortality trade-off is expressed as the proportion dying per year (due to reproduction) if the proportion of the surplus energy devoted to reproduction is u_x at age x. The functional form of this relationship is given by eq 6. Data sources are given in Table 1.

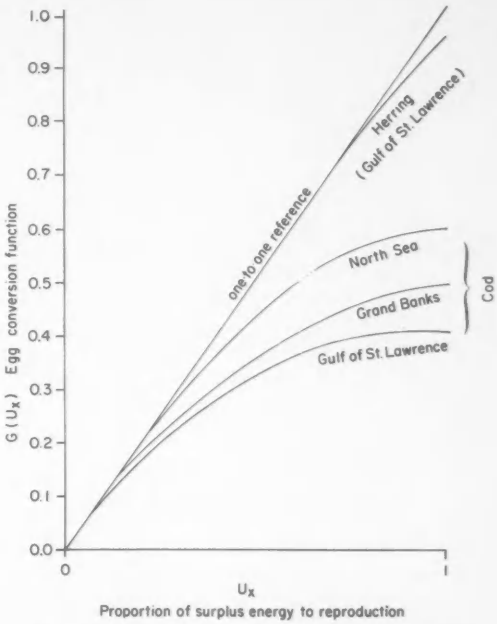

FIG. 2. Predicted egg conversion functions, $g(u_x)$, if the proportion of surplus energy devoted to reproduction is u_x at age x under the assumption that the observed life history is evolutionarily stable. The functional form of the relationship is given by eq 7. Data sources are given in Table 1.

3) The result of 2 was normalized by multiplying the partial derivative by the ratio of the parameter to the predicted value of Q_a, C_1, Q_b, or C_2. (see Table 2, normalized).

The effect of the normalizations is to reduce all the analyses to the same scale, so that the entries in the table show the proportion change in the predicted values of Q_a, C_1, Q_b, or C_2 from a proportional change in α, β, or T. That is, the first value in Table 2 (normalized) is

$$\frac{\alpha}{Q_a}\left(\frac{\partial Q_a}{\partial \alpha}\right).$$

The result is a matrix of values showing the quantitative change in a component, i.e. its sensitivity, to a particular state variable. An illustration of the sensitivity analysis applied to the southern Gulf of St. Lawrence stock of Atlantic cod is shown in Table 2. The parameters γ_1 and γ_2 (see eq 4 and 5) were least sensitive to incorrect parameter estimation. To simplify the sensitivity analysis and interpretation, γ_1 and γ_2 were held constant at 2.5 and 1.8, respectively.

Incorrect Estimation of Surplus Energy Parameters

The effects of variations of α with β held constant and with variations of β with α held constant were calculated. The results of the sensitivity analysis (Table 2) indicate that the estimates of natural mortality are particularly sensitive to incorrect parameter estimations of the surplus energy parameter β and relatively less sensitive to α. The reproduction–mortality trade-off is relatively more sensitive than the egg conversion function parameter to incorrect parameter estimation.

Incorrect Estimation of the Maximum Age

It is difficult to estimate the natural life span of an exploited stock because of the drastic change in the mortality such populations usually face. Some of the estimates of maximum age in Table 1 are little more than guesses. However, estimates of natural mortality are not very sensitive to incorrect parameter estimation of maximum age (Table 2). Estimates of reproduction–mortality trade-offs and egg conversion functions are relatively more sensitive to such incorrect parameter estimations.

Density-Dependence

Thus far we have discussed only density-independent models. For the density-dependent case, Charlesworth and León (1976) have shown that the evolutionarily stable life history is the solution to a maximization problem if the population reaches demographic equilibrium. Letting survivorship and fecundity be functions of density, N, they showed that the evolutionarily stable life history corresponds to the $l_x(N)$ and

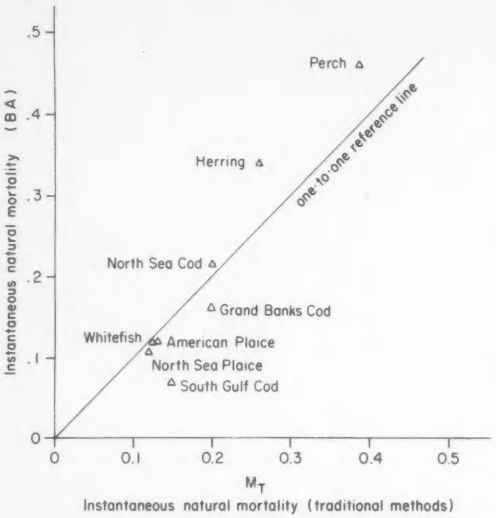

FIG. 3. Instantaneous natural mortality rates obtained from traditional methods (see references in Table 1) compared with the instantaneous BA estimate of natural mortality under the assumption that postmaturational growth is due to a concave egg conversion function.

$m_x(N)$ schedule that maximized N. That is, for any other schedule, $l_x'(N)$ and $m_x'(N)$, at equilibrium

$$(10)\quad \sum_x l_x'(N)m_x'(N) < \sum_x l_x(N)m_x(N) = 1.$$

The sensitivity of our estimates depends crucially on whether density-dependent factors affect juveniles or adults. The most important density-dependent factors usually affect prerecruit mortality (Beverton and Holt 1954; Ricker 1954). If this is the case, the estimates of growth and maturation size will not change, and the inequality in eq 10 would be adequately approximated by the inequality in eq 1 (if r is assumed to be 1). If density-dependent mortality occurs before the age at which reproduction can occur (e.g. in the larval stage), then the estimates of postmaturational natural mortality would be virtually unaffected. This can be seen by considering that this prereproduction mortality must be experienced no matter what size the fish matures. Similarly, if the main effect of density-dependence was on larval growth (Ware 1975), there would be a small change in the growth rate (eq 2) but this will not have a major effect on the mortality estimates.

If there is strong density-dependence on adult growth rates and mortality rates, then the estimates obtained using the assumption of density-independence must be considered as first approximations. Better density-dependent estimates can be obtained if density-dependent relationships for growth, reproduction, and recruitment are known. In this case, the growth and reproduction schedules can be determined at demographic equilibrium, and the inverse optimization procedure can be directly applied.

The key assumption in the application of eq 10 is that demographic equilibrium is reached. This may not be true because of either an inherent tendency of some populations to oscillate or because environmental variability never allows the population to remain at equilibrium. If there are large stochastic variations in adult growth rates, the inequality in eq 10 must be replaced by a fitness criterion that depends on that stochasticity (Gillespie 1977). Inverse optimization methods can also be applied in this case to examine the possibility of density-dependent adult mortality rates.

TABLE 2. Sensitivity analysis showing the effects of variations in surplus energy parameters (α and β) and the maximum life span (T) on the predicted evolutionarily stable mortalities (Q_a and Q_b), reproduction mortality trade-off parameters (C_1 and γ_1), and egg conversion function parameters (C_2 and γ_2). Data are for southern Gulf of St. Lawrence Atlantic cod (Ware 1980).

	Q_a	C_1	Q_b	C_2
		Unnormalized		
α	0.013	−0.051	0.020	−0.141
β	1.50	−4.92	1.53	−6.10
T	0.0036	−0.019	0.0025	−0.32
		Normalized		
α	1.35	−2.26	2.00	−1.61
β	12.2	−15.0	12.9	−5.0
T	1.37	−3.26	1.09	−1.43

Discussion and Implications for Management

Sequential population analysis depends on the accurate estimation of natural mortality (Gulland 1965; Pope 1972). Our methods provide independent estimates of natural mortality, which are derived from an entirely different body of data by different assumptions and techniques. The BA estimator is, of course, subject to its own suite of biases and uncertainties. Fortunately, the numerical values of the mortality estimates are not particularly sensitive to which biological constraint causes postmaturational growth.

Beverton and Holt (1959) were the first to systematically study the association between natural mortality and other life history traits (growth rate, asymptotic length, and longevity). Pauly (1980) has carried this empirical approach in another direction with his regression analysis of natural mortality on asymptotic size, growth rate, and the mean environmental temperature in 175 fish stocks. Jones and Johnston (1977) explicitly invoked evolutionary arguments for these empirical relationships. They used a simulation model to establish upper and lower limits for natural mortality in several gadoid species.

Our method cannot be used with precision for short-lived species (less than 4 yr) that spawn only during a short period during an annual cycle. For such species, a plot of fitness versus age at maturation would peak at 1 yr for a wide range of mortalities, and the inverse optimization procedure would not yield precise estimates. This is not true for longer lived species or multivoltine species (Myers and Runge 1983). If our method is to be used for very short-lived species, which form the bulk of the catch in some tropical fisheries (Pauly 1979), the surplus energy must include a seasonal component.

We have compared our method of estimating natural mortality with estimates using traditional methods (Fig. 3). The difficulty with testing our method is that traditional methods of natural mortality are not very accurate. To remedy this, the BA method has been tested with field data on seasonal changes of natural mortality in the copepod *Acartia clausii* (Myers and Runge 1983). The predicted natural mortality showed excellent agreement with the field estimates of Landry (1978), who obtained 86 separate estimates of adult mortality.

The BA estimate of natural mortality in most cases gives similar predictions to estimates based on population dynamic measurements (Fig. 3). There are situations in which traditional estimates of natural mortality are unavailable (e.g. because of lack of a sufficiently long series of age−frequency data). In these cases the BA estimator can provide estimates of natural mortality based on data from one or two collections. Even when estimates of natural mortality are available, the BA estimator provides a method of testing whether they are consistent with other life history information on the species.

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Effects of Changes in pH on Transparency and Thermal Regimes of Lohi Lake, near Sudbury, Ontario

NORMAN D. YAN

Ontario Ministry of the Environment, Water Resources Branch, Limnology Section, P.O. Box 213, Rexdale, Ont. M9W 5L1

YAN, N. D. 1983. Effects of changes in pH on transparency and thermal regimes of Lohi Lake, near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 40: 621–626.

Changes in Secchi transparency (depth) and thermal regimes accompanying experimental neutralization and subsequent re-acidification of Lohi Lake, near Sudbury, Ontario are described. Secchi depth was not correlated with chlorophyll concentrations, phytoplankton biomass or total phosphorus, but it was negatively correlated with pH. Secchi depth was positively correlated with thermocline depth, epilimnetic thickness, and hypolimnetic heating rates suggesting that acidification should result in deeper mixing zones and warmer hypolimnia in lakes. Several possible implications of changes in transparency and thermal regimes produced by acidification are presented.

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On décrit dans l'article qui suit les changements dans la transparence mesurée au disque de Secchi (profondeur) et dans les régimes thermiques qui ont accompagné une neutralisation et une réacidification subséquente expérimentales du lac Lohi, près de Sudbury, en Ontario. La profondeur du disque de Secchi n'est pas liée aux concentrations de chlorophylle, biomasse phytoplanctonique ou phosphore total, mais est en corrélation négative avec le pH. La profondeur du disque de Secchi est en corrélation positive avec la profondeur de la thermocline, l'épaisseur de l'épilimnion et les taux de réchauffement de l'hypolimnion, ce qui donne à penser que l'acidification devrait résulter en des zones de mélange plus profondes et des hypolimnions plus chauds dans le lac. Nous décrivons plusieurs implications possibles de changements dans la transparence et les régimes thermiques causés par l'acidification.

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ONE phenomenon that apparently accompanies the acidification of fresh waters is an increase in transparency. Almer et al. (1974) indicated that the pH of (lake) Stora Skarsjön fell from 6.2 to 4.5 between 1943 and 1973. The transparency increased from 3 to 10 m over the same time period. Schofield (1972) compared transparencies measured from 1950 to 1953 with those measured in 1967 in 14 lakes in the Adirondack Mountains of New York. Mean Secchi transparency increased from 5.6 to 8.3 m while mean pH fell from 5.9 to 5.0. Schindler (1980) and Malley et al. (1982) observed that the transparency of Lake 223 in northwestern Ontario increased when the lake pH was experimentally depressed from 6.6 to 5.6.

Kramer (1978) suggested that the increase in transparency in acidified lakes was in part attributable to decreases in water column levels of particulate organic matter because of reduced phytoplankton productivity. Almer et al. (1978) suggested that increased transparency was attributable to precipitation of yellow organic acids (YOA) by Al at low pH. I examine these alternate hypotheses in this study.

The influence of increased transparency on the thermal regimes of lakes acidified by the atmospheric deposition of strong acids has not been investigated, although Malley et al. (1982) observed that experimental acidification depressed the thermocline of Lake 223 in northwestern Ontario. Therefore, the second purpose of this study was to investigate whether thermal regimes of lakes change when the transparency increases because of acidification.

The thermal regime of a lake is influenced by many factors in addition to transparency, including latitude, altitude, volume, area, fetch and depth of the lake, topography of the watershed as a modifier of the velocity of surface winds, and net radiation influx. Consequently, it is difficult to attribute differences in thermal regimes among lakes to specific causes. In this report, I describe the transparency and selected aspects of the thermal regime of a single lake, Lohi Lake, near Sudbury, Ontario. Prior to experimental neutralization in the fall of 1973, the pH of Lohi Lake was 4.4. The pH was maintained at >6.0 by further small additions of base in 1974 and 1975, but it subsequently declined, reaching 4.74 by 1979 (Dillon et al. 1979; Yan and Dillon 1983). Use of data from a single lake permits examination of the influence of changes in pH on transparency and on thermal regimes in a situation in which morphometric and geographic considerations can be ignored.

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Description of Lohi Lake

Lohi Lake is located 11 km south of Sudbury at 46°23′N and 81°02′W. It has a mean depth of 8.3 m, a maximum depth of 19.5 m, a fetch of 1.6 km, and a surface area of 40.6 ha. Scheider et al. (1975) described the chemistry and biota of the lake in 1973, prior to additions of base. At that time the lake was acidic (pH 4.4), and contaminated with Cu (84 mg m^{-3}) and Ni (250 mg m^{-3}). The lake's oligotrophic nature was indicated by low levels of total phosphorus (6.1 mg TP m^{-3}), a high total nitrogen to TP ratio (44 by weight) and transparent waters (Secchi depth of 8.8 m). Scheider et al. (1975), Dillon et al. (1979), Dillon and Scheider (1982) and Yan and Dillon (1983) summarized changes in chemistry and biota accompanying additions of base to the lake.

Methods

All lake samples were collected at weekly intervals over the ice-free season and were volume-weighted composites of the entire lake for pH and TP and through a depth corresponding to twice the Secchi transparency (23 cm diam) for phytoplankton and chlorophyll. Methods of collection and analysis of chemical and phytoplankton samples are given by Scheider et al. (1975) and Yan (1979), respectively.

Temperature was measured at 1-m intervals to 1 m above the sediment surface at the deepest point in the lake with a YSI model 432D telethermometer from 1973 to 1976 and subsequently with a Montedoro–Whitney TC-5C thermister. The thermisters were calibrated at least twice a year against a thermometer meeting National Bureau of Standards requirements for accuracy. The depth of the boundary of the epilimnion and metalimnion, considered to represent epilimnetic thickness, was taken from the first inflection point of temperature vs. depth plots. A thermocline was considered to exist whenever the change in temperature from the lake surface to the bottom was >4°C. The thermocline was a plane located at the depth where the change in temperature with depth ($d\theta/dz$) was maximum or at the midpoint of the depth zone through which $d\theta/dz$ was constant and a maximum. The depth of the plane delineating the top of the hypolimnion was determined graphically. It was assumed to be located at the depth at which two straight lines intersected, one through the thermocline with slope equal to $d\theta/dz$ at the thermocline, the second through temperatures observed 1 and 2 m above the bottom.

Surface wind speeds and numbers of hours of bright sunshine were taken from the Environment Canada meteorological station located at the Sudbury Airport.

Results

Transparency

Secchi transparency (depth), averaged over the ice-free season in Lohi Lake varied from 5.6 to 9.3 m. It was not correlated with TP ($r^2 = 0.19$, $P > 0.1$) with chlorophyll a ($r^2 = 0.01$, $P > 0.1$) or with phytoplankton biomass ($r^2 = 0.03$, $P > 0.1$, Table 1). A linear regression analysis indicated that Secchi depth (in metres) was negatively correlated with pH:

$$(1)\quad \text{Secchi} = 17.63 - 1.97\ \text{pH} \qquad r^2 = 0.86,\ P < 0.01$$

Thermal Regimes

Isotherm diagrams for Lohi Lake from 1973 to 1979 are provided elsewhere (Ontario Ministry of the Environment 1982). There were differences between years in five parameters calculated from the temperature data: epilimnetic thickness (z_e), thermocline depth (z_t), depth of the hypolimnetic surface (z_{hypo}), hypolimnetic temperature (θ_{hypo}) and hypolimnetic heating rate. Comparing midsummer values of these parameters, z_e, z_t and z_{hypo} were smallest when lake pH was high and Secchi transparency low (Table 1). They were related to Secchi depth (in metres) and pH as follows:

$$(2)\quad z_e = 4.51 + 0.62\ \text{Secchi} \qquad r^2 = 0.58,\ P < 0.05$$

$$(3)\quad z_e = 17.17 - 1.54\ \text{pH} \qquad r^2 = 0.79,\ P < 0.01$$

$$(4)\quad z_t = 6.04 + 0.57\ \text{Secchi} \qquad r^2 = 0.47,\ P < 0.10$$

TABLE 1. Variations between years in pH, chlorophyll a, Secchi depth, TP, phytoplankton biomass, z_e, z_t, θ_{hypo}, and hypolimnetic heating rate in Lohi Lake. Values are ice-free period means except where otherwise indicated.

Year	pH	Chlor a (mg m^{-3})	Secchi depth (m)	TP (mg m^{-3})	Phyto. biomass (mg L^{-1})	z_e[a] (m)	z_t[a] (m)	θ_{hypo}[b] (°C)	Heating rate[c] (°C d^{-1})	z_{hypo}[a]
1973	4.4	1.7	8.8	6.1	0.65	10.2	11.2	12.6	0.045	12.5
1974	6.04	0.9	5.6	5.0	0.44	8.8	10.0	9.2	0.026	10.0
1975	6.09	1.3	5.7	3.7	0.25	7.3	8.47	7.4	0.016	10.0
1976	6.09	1.3	5.7	5.4	0.24	7.1	8.25	8.9	0.022	10.5
1977	5.27	1.2	6.9	7.3	0.32	9.6	10.6	8.9	0.032	11.5
1978	4.79	0.70	9.3	5.6	0.13	9.5	10.3	9.6	0.046	11.5
1979	4.74	0.83	7.6	5.7	0.57	10.0	11.5	10.6	0.049	12.5

[a]Mean for July and August.
[b]Mean temperature at 14 m for June to September.
[c]Slope of a linear regression equation with temperature at 14 m being the dependent variable and the independent variable being accumulated time since establishment of the hypolimnion.

TABLE 2. Level of significance[a] of *t*-tests of differences between years pairing months (May to October) for average wind speed (km h^{-1}) and numbers of hours of bright sunshine (h mo^{-1}), the latter in parentheses. Mean May to October values are included. Data from Environment Canada, Meteorological Station at the Sudbury Airport.

			Level of significance					
Wind speed	Bright sun	Year	1974	1975	1976	1977	1978	1979
17.7	199	1973	—	0.05	0.05	—	—	0.01
17.9	190	1974		(0.05)	(0.05)	—	—	0.01
20.2	243	1975			—	—	—	0.01
18.9	232	1976				—	—	0.05
18.7	223	1977					—	0.01
18.0	226	1978						0.05
15.5	215	1979						—

[a] $P < 0.05$ only.

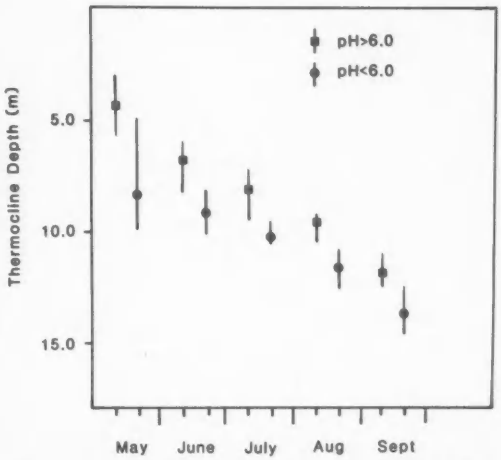

FIG. 1. Seasonal variation in average monthly thermocline depth (z_t) in Lohi Lake. The solid square is the mean of years when lake pH was >6.0 (1974–76). The solid circle indicates the mean of years when lake pH was <6.0 (1973, 1977–1979). Range of monthly means indicated by vertical bar.

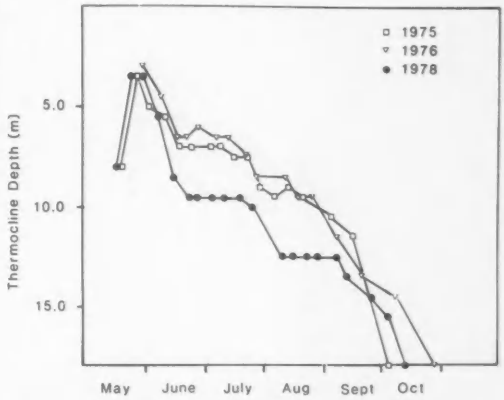

FIG. 2. Seasonal variation in thermocline depth (z_t) in 1975, 1976, and 1978 in Lohi Lake.

(5) $z_t = 18.04 - 1.49\ \text{pH}$ $\quad r^2 = 0.74,\ P < 0.02$

(6) $z_{hypo} = 7.26 + 0.56\ \text{Secchi}$ $\quad r^2 = 0.64,\ P < 0.05$

(7) $z_{hypo} = 18.73 - 1.41\ \text{pH}$ $\quad r^2 = 0.90,\ P < 0.01$

A positive correlation between epilimnetic thickness and average wind speed might have been anticipated, but a negative correlation ($r^2 = 0.52$) was observed. In 1975 and 1976 when the epilimnion was thinnest, average wind speeds and surface irradiances were actually higher than in all other years. In 1979 when the epilimnion was relatively thick, results of paired *t*-tests indicated that average wind speed was significantly lower than in all other years (Table 2).

It is possible that any correlation, for example the negative correlation observed between summer z_t or z_t and pH is spurious. Average wind speeds were not higher in 1973 and 1977 to 1979 when the lake pH was depressed, but spring weather conditions would have determined the depth at which the thermocline was first established in the lake, and this could influence summer thermocline depths. Examination of seasonal patterns of downward migration of z_t in Lohi Lake supported this possibility. The thermocline was established at shallower depths, on average, in the spring of 1974 to 1976 when lake pH was >6.0, than in subsequent years when lake pH fell (Fig. 1). This correlation between pH and spring thermocline depth indicates either that the correlation between summer thermocline depth and pH is spurious or that acidification influences the initial as well as the summer depth of stratification.

To examine whether pH influenced z_t in summer it was therefore necessary to examine a subset of the data having similar z_t in the spring. Three such years existed, 1978 data when lake pH was 4.79, and 1975 and 1976 data when lake pH was 6.09 (Table 1). The thermocline was located at a depth of 3–3.5 m in late May in these years (Fig. 2).

Despite the similarity in May thermocline depths, z_t

TABLE 3. Comparison of maximum hourly wind speeds (km h^{-1}) and hours of bright sunshine (h mo^{-1}) observed in selected months of 1975, 1976, and 1978 at the Sudbury Airport.

	Wind speed			Sunshine		
Month	1975	1976	1978	1975	1976	1978
May	45	47	48	272	229	277
June	42	48	44	296	294	270
July	51	50	41	319	284	276
August	45	56	59	294	282	284
September	40	56	59	139	194	137
October	51	52	48	137	112	113

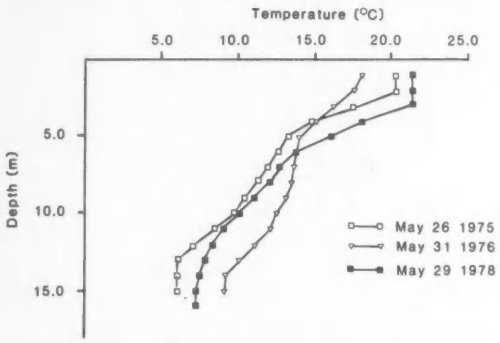

FIG. 3. Vertical temperature profiles in Lohi Lake in the last week of May in 1975, 1976, and 1978.

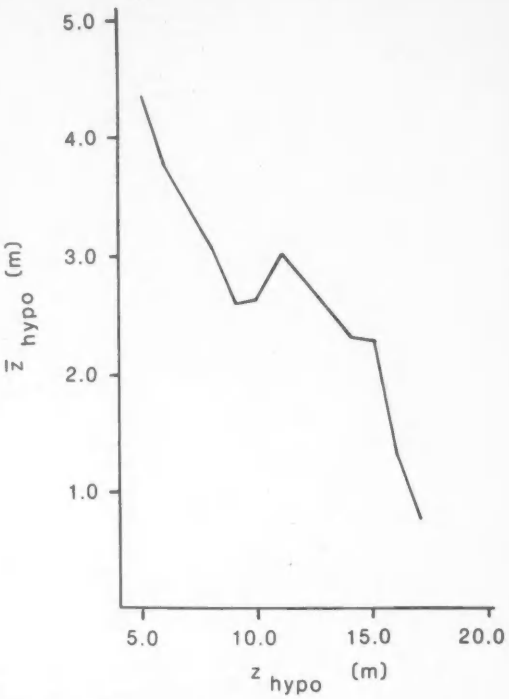

FIG. 4. The relationship between mean hypolimnetic thickness ($\bar{z}_{hypo}$) and depth of the hypolimnetic surface (z_{hypo}) in Lohi Lake. Values were calculated from morphometric data.

migrated downward more rapidly in 1978 than in the other two years so that when it was stable, the thermocline was much deeper in 1978 (Fig. 2). The difference was established in June and July even though winds were not apparently stronger nor insolation higher in these months in 1978 than in 1975 and 1976 (Table 3). Hypolimnetic water temperatures in late May of 1978 were between those observed in late May of the two years when lake pH was >6.0 (Fig. 3). This suggests that the deeper z_r in the summer of 1978 was not attributable to a deeper z_r in the spring nor to smaller temperature-dependent density gradients through the metalimnion. This comparison indicated that while conditions of spring stratification played an important role in subsequent depths of thermoclines in Lohi Lake, other factors, most probably transparency, were also important.

Hypolimnetic heating rate (in °C d^{-1}) and temperature were also correlated with transparency in Lohi Lake (Table 1); however, the relationship between Secchi depth and hypolimnetic temperature (θ_{hypo}) was weak:

$$(8)\quad \text{Heating rate} = 0.0075\ \text{Secchi} - 0.02 \qquad r^2 = 0.79,\ P < 0.05$$

$$(9)\quad \theta_{hypo} = 0.73\ \text{Secchi} + 4.41 \qquad r^2 = 0.48,\ P < 0.10$$

Variations in weather were probably not responsible for the changes in hypolimnetic thermal regimes. In 1975 and 1976 heating rates and temperatures were lower than in all other years (Table 1), yet radiation input, as estimated from numbers of hours of bright sunshine mo^{-1}, and average wind speeds were higher in these two years than in all other years (Table 2).

Discussion

The Lohi Lake data support the observations of Almer et al. (1974), Schofield (1972), and Schindler (1980) that acidification of lakes results in increased transparency. This suggests that the strong negative correlation between pH and Secchi transparency noted by Hörnström et al. (1973) and Anon. (1978) does not indicate simply that clearer lakes are more susceptible to acidification. Undoubtedly the transparency increased when these lakes acidified.

Different mechanisms have been proposed to explain this increase in transparancy. Kramer (1978) suggested that it was attributable to the dissolution of Fe and Mn colloids and decreases in organic detritus because of reduced phytoplankton productivity. For Lohi Lake, average annual Secchi depth was correlated with pH ($r^2 = 0.86$) but not with phytoplankton biomass or chlorophyll *a*. Hence increased transparency was not attributable to reduced biomass of phytoplankton. Hörnström (1979), Dillon et al. (1979), and

Schindler (1980) have indicated that phytoplankton productivity (expressed volumetrically) is not reduced by acidification. Thus, available data do not support Kramer's suggestion that increased transparency is attributable in part, to reduced activity of primary producers.

Almer et al. (1978) noted that the color of an aqueous solution of yellow organic acid (YOA) was lowest at pH ~4.8 with addition of 1 mg L^{-1} of Al, and increased at both higher and lower pH levels. They suggested that increased clarity in acidic lakes was attributable to precipitation of YOA by Al. Schnitzer and Kahn (1972) had previously reported that at low pH, high concentrations of Al and Fe would coagulate and subsequently precipitate humic acids. These observations are consistent with the observed threefold decrease in organic matter that accompanied the acidification and increased transparency of (lake) Stora Skarsjön (Almer et al. 1974). However, increases in transparency can also occur without precipitation of organic matter. Schindler (1980) noted that the increase in transparency of experimentally acidified Lake 223 in northwestern Ontario was not accompanied by a decrease in dissolved organic carbon levels or phytoplankton biomass. This suggests that the increased transparency was caused not by precipitation of YOA, but by reduction in their color. This hypothesis, however, is not consistent with the observation of Gjessing (1976) that the color of aqueous, humic acid solutions were quite stable over a pH range of 4 to 7. Clearly, a universal explanation for the increase in transparency in acidified lakes is not yet available. The cause is, however, not reduced phytoplankton biomass.

Harvey et al. (1981) observed that mosses grew at greater depths in acidic than in nonacidic lakes in Ontario. Almer et al. (1978) and Schindler (1980) observed that phytoplankton biomass and productivity might increase in acidified lakes when the euphotic zone deepened. Increases in transparency may, therefore, be very important for primary producers in acidified lakes.

Temperature

Examination of a subset of the Lohi Lake data with similar spring thermocline depths indicated that summer thermocline depths of lakes may be depressed should the lakes acidify. Similarly, Malley et al. (1982) observed that the epilimnetic thickness of Lake 223 in northwestern Ontario increased after the lake was experimentally acidified.

Epilimnetic thickness will increase at constant lake surface wind speeds if the temperature, i.e. the density gradient across the metalimnion, decreases. Therefore, an increase in hypolimnetic temperature produced from deep solar heating in Lohi Lake (to be discussed) could have been responsible for the positive correlation between transparency and epilimnetic thickness. The average summer epilimnetic temperature in Lohi Lake was 22°C. A change in hypolimnetic temperature such as that observed between 1973 (12.6°C) and 1975 (7.4°C, Table 1) would have reduced the density difference through the metalimnion by about 5×10^{-4} g cm^{-3}, or 25%, assuming a 22°C epilimnion (Cole 1975).

Scheider et al. (1975) noted that the midsummer bottom water temperatures of Clearwater Lake (z_{max} = 21 m), an acidified (pH 4.4) lake near Sudbury, were 11 to 14°C. N. Conroy (unpublished data) has noted temperatures of 9–11°C at 42 m in Nellie Lake and 11°C at 33 m in Florence Lake, both acidified lakes (pH ~4.5) in northeastern Ontario. Bottom water temperatures in Shield lakes of these depths are more typically 4–6°C. As might have been anticipated from these observations, the hypolimnetic heating rates and temperatures of Lohi Lake were greatest when the lake was acidic. There was no relationship between profundal water temperatures in the spring and pH.

Hypolimnetic heating rates and temperatures may increase following acidification for two reasons. Transparency increases; hence, direct solar heating of deep waters may increase. Alternatively, a reduction in hypolimnetic volume (V_{hypo}) to surface area (A_{hypo}) ratio must increase the rate of hypolimnetic heating at constant molecular and turbulent heat transfer rates to the hypolimnion. The mean depth of the hypolimnion, $\bar{z}_{hypo}$, is equivalent to V_{hypo}/A_{hypo}.

In Lohi Lake, z_{hypo}, the depth of the hypolimnetic surface varied from 10 to 12.5 m in midsummer (Table 1). Over a range in z_{hypo} of 9 to 13 m, z_{hypo} and $\bar{z}_{hypo}$ are actually independent in Lohi Lake (Fig. 4). There was no correlation between $\bar{z}_{hypo}$, i.e. V_{hypo}/A_{hypo} and hypolimnetic heating rate ($r^2 = 0.05$, $P > 0.1$). This suggests that increases in hypolimnetic heating rates in Lohi Lake in years when the lake was acidic, was not attributable to reduction in $\bar{z}_{hypo}$. Hence, the most probable primary cause of the increase in hypolimnetic heating rate following re-acidification of the lake is increased direct solar heating of the hypolimnetic waters because of increased light penetration.

Increased hypolimnetic heating rates in acidified lakes must have other consequences. As previously indicated, the entrainment of the hypolimnion into the epilimnion must be more rapid after acidification because of a reduced density gradient through the metalimnion. Instantaneous rates of zooplankton community production are temperature dependent and may increase. Hypolimnetic oxygen may be depleted more rapidly because hypolimnetic volume decreases and because warmer temperatures may increase rates of organic matter decomposition. On the other hand, the severity of hypolimnetic oxygen depletion may be reduced because of earlier autumnal overturn and because the trophogenic zone may extend into the hypolimnion, permitting photosynthetic generation of oxygen within it. Acidification, therefore, may have indirect effects on biota operating through changes in transparency and thermal regimes.

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Energy Metabolism in a Rapidly Developing Marine Fish Egg, the Red Drum (*Sciaenops ocellata*)[1]

RUSSELL D. VETTER AND ROBERT E. HODSON

Department of Microbiology, University of Georgia, Athens, GA 30602, USA

AND CONNIE ARNOLD

University of Texas Marine Institute, Port Aransas, TX 78373, USA

VETTER, R. D., R. E. HODSON, AND C. ARNOLD. 1983. Energy metabolism in a rapidly developing marine fish egg, the red drum (*Sciaenops ocellata*). Can. J. Fish. Aquat. Sci. 40: 627–634.

Rates of utilization of different lipid classes, glycogen, protein, and adenine nucleotides in the eggs of red drum (*Sciaenops ocellata*) were measured concurrently throughout embryonic development. Red drum eggs are small, pelagic, and very rapidly developing, going from fertilization to hatching in as little as 19 h at natural spawning temperatures. Wax esters comprised about 50% of the neutral lipid reserve along with triglyceride. Lipid was quantitatively the most important energy reserve supplying virtually all of the catabolic demand. Total lipid content decreased 30% from 23.6 to 16.6 mg/g during development. Glycogen decreased 53% from 0.279 to 0.103 mg/g. Protein did not contribute to catabolism. Total adenylates, primarily ATP, decreased from 564 to 271 nmol/g. Adenylate energy charge decreased from 0.87 to 0.58. Glycogen and lipid were used concurrently rather than sequentially during development. The rapid rate of development could be accounted for by simple thermal effects on metabolism rather than any unique biochemical adaptation. High concentrations of wax ester may be an adaptation for maintaining buoyancy at reduced salinities.

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Les taux d'utilisation de différentes classes de lipides, de glycogène, de protéines et d'adénine-nucléotides dans les oeufs de tambour rouge (*Sciaenops ocellata*) ont été mesurés concurremment tout au long du développement embryonnaire. Les oeufs de cette espèce sont petits, pélagiques et se développent très rapidement, la durée du développement, depuis la fécondation jusqu'à l'éclosion, aux températures de fraie naturelles pouvant être aussi courte que 19 h. Les cires constituent environ 50 % de la réserve de lipides neutres, avec les triglycérides. Les lipides sont quantitativement la plus importante réserve énergétique, répondant à presque toute la demande catabolique. La teneur en lipides totaux diminue de 30 %, passant de 23,6 à 16,6 mg/g, au cours du développement. Le glycogène diminue de 53 %, soit de 0,269 à 0,103 mg/g. Les protéines ne contribuent pas au catabolisme. Les adénylates totaux, en grande partie ATP, diminuent et passent de 5,64 à 271 nmol/g. La charge énergétique d'adénylates passe de 0,87 à 0,58. Le glycogène et les lipides sont utilisés concurremment plutôt que successivement pendant le développement. On peut expliquer le taux de développement rapide par simples effets thermiques sur le métabolisme plutôt que par une adaptation biochimique. Il se peut que les fortes concentrations de cire soient une adaptation en vue de maintenir la flottabilité dans des salinités réduites.

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THE biochemical energy reserves of a teleost egg are finite and must supply all of the metabolic energy needed for embryonic development. Thus, measurement of the types, amounts, and regulation of consumption of endogenous energy stores in developing eggs is fundamental to understanding the timing of embryonic development and predicting the effects of environmentally induced metabolic stress on development and hatching success. On a caloric basis, neutral lipid is generally considered to be the most important energy reserve in teleost eggs, but protein and carbohydrate can also be important in some species (see reviews by Williams 1967; Blaxter 1969;

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Terner 1979; Boulekbache 1981). Although often referred to as energy storage compounds, e.g. Boulekbache (1981), the adenine nucleotides (adenosine triphosphate (ATP), adenosine diphosphate (ADP), and adenosine monophosphate (AMP)) contain very little "stored" energy relative to lipid or carbohydrate due to their low concentrations in cells. However, the importance of ATP as a transducer of energy from storage compounds to energy requiring cell functions and the role of adenine nucleotides in regulating energy production and utilization suggest that adenine nucleotides should also be an important component of any study of overall energy metabolism in teleost eggs. A high concentration of ATP relative to ADP and AMP indicates a large pool of immediately available energy which inhibits glycolysis and stimulates gluconeogenesis and presumably growth. A low concentration of ATP relative to its breakdown products, ADP and AMP, indicates that energy production is not keeping pace with energy utilization and allosterically stimulates mobilization of glycogen (glycogenolysis) and the regeneration of ATP through glycolysis and the tricarboxylic acid (TCA) cycle. Atkinson (1968, 1977) proposed that cells regulate their energy metabolism based on the ratio of the three adenylates expressed as the adenylate energy charge (EC), a single value varying from 0.0 to 1.0 based on the equation

$$EC = \frac{ATP + \frac{1}{2}ADP}{ATP + ADP + AMP}.$$

In a "normal" free-living organism, when energy-yielding (catabolic) and energy-consuming (anabolic) pathways are in balance, EC is usually between 0.84 and 0.95 (Atkinson 1977). EC ratios below 0.80 have generally been interpreted as indicative of metabolic stress (Atkinson 1977; Ivanovici 1980; MacFarlane 1981; Vetter and Hodson 1982). In a developing fish egg there is an apparent conflict, in terms of metabolic control, in the sense that the egg is "starving" (no exogenous supply of energy), yet it must rapidly synthesize new tissue. Adenylate ratios may not function in the expected way under these conditions.

To date, knowledge of energy reserves and energy metabolism in developing fish eggs has been based primarily on studies of single classes of compounds in relatively slowly developing, large, demersal eggs of such species as salmon, trout, and loach, notable exceptions being the studies of Pacific sardine (*Sardinops caerulea*) by Lasker (1962) and striped bass (*Morone saxatilis*) (Eldridge et al. 1981). In fact, no study has ever measured concurrent changes in lipid, protein, glycogen, and adenylates during development of a teleost egg. As the eggs of more marine teleosts are identified and the types of eggs and rates of development studied, it is becoming clear that small, buoyant eggs are the predominant form of reproductive product and that particularly in warmer waters, many of these small eggs are also extremely rapidly developing (Blaxter 1969; Russell 1976; Arnold et al. 1977).

To better understand the developmental requirements and potential susceptibility to different environmental stresses of these type of eggs, we have begun to measure aspects of the energy metabolism of eggs of red drum (*Sciaenops ocellata*), a warmwater, estuarine-dependent sciaenid species, which can be naturally induced to spawn in captivity (Arnold et al. 1977). The red drum is an economically important species along the southern Atlantic coast of the United States and throughout the Gulf of Mexico. It spawns repeatedly, producing large numbers (about 10^6 per spawn) of small (0.86–0.98 mm), buoyant eggs. These pelagic eggs, which are presumably exposed to intense predation pressure, develop extremely rapidly, going from fertilized egg to hatched larvae in 19–29 h depending on spawning temperature (Arnold et al. 1977; Holt et al. 1981b). In this study, eggs developed in about 22 h. We have measured concurrent changes in neutral lipid (triglyceride and wax ester) and carbohydrate (in the form of glycogen) throughout an 18-h period from immediately after fertilization to immediately prior to hatching. We have also measured pool sizes of primarily structural compounds that could also serve as potential energy reserves. These included protein, phospholipids, and cholesterol. Adenylate concentrations and ratios were measured as a first step in determining the role of these compounds in regulating lipid and glycogen metabolism during egg development.

Methods

The spawning tanks, spawning procedure, and morphology of red drum eggs are described in detail elsewhere (Arnold et al. 1977; Holt et al. 1981b). In brief, four to six adult fish of approximately 10–14 kg were kept in 29.9-kL holding tanks and brought into spawning condition through adjustment of photoperiod and temperature. Although spawning occurs in darkness, it is believed that each night's spawn was the result of a single female, since hydration of the eggs produces a noticeable swelling of the abdomen during the evening preceding spawning. Spawns occurred every 2–3 d. Although it has been reported that egg size and nutritional quality can vary with adult size, age, body condition, season, salinity, and whether the spawn was artificially induced (see review by Blaxter 1969; Kuznetsov and Khalitov 1979), the controlled conditions, high rate of feeding, similarity of female size, and natural inducement of spawning resulted in the production of eggs of similar size and nutritional quality during this study. Eggs from different spawns were used to develop methods and to determine typical levels of the different compounds. Since it was impossible to determine exact time of spawn (only first appearance in the collection box), it was impossible to group several spawns without confounding the time-dependent variables. The results reported here are from synoptic samples of a single spawn from a single female. Results presented here for concurrent measurements of different reserves were typical in all respects to preliminary measurements of individual compounds in other previous spawns.

Spawning occurred at about 1:00 a.m. at 23°C and 36‰ in August; approximately 10^6 eggs were produced. Eggs began to hatch 22 h after they appeared in the collection box, with a hatching success of over 95%. Based on previous studies with the spawning tanks it is believed that eggs appear in the collection box from 10 to 30 min after spawning occurs. As many samples and replicates were taken as was permitted by the size of the total spawn. Each sample weighed about 1 g and represented about 200 eggs. Total wet weight of the eggs did not change after chorion hardening, and results are

expressed on a wet weight basis. The buoyant eggs were skimmed from the holding tanks at 0.5, 4, 12, and 18 h after spawning and fertilization had occurred. Samples taken at 0.5 and 4.0 correspond approximately with first cell division and gastrula, 12 h with formation of notochord, optic vesicles, melanophores, and elongation of the tail, 18 h with complete differentiation of brain, elongation and separation of tail from the oil droplet, and flexing of the tail. The times of 0.5–4, 12, and 18 h correspond to the early, middle, and late stage of development, respectively, described by Holt et al. (1981b).

Eggs were drained on 200-μm Nytex® screen and immediately plunged into liquid nitrogen (−190°C). Rapid freezing is critical for the accurate determination of labile compounds such as ATP (see Faupel et al. (1972) for a detailed analysis of this problem). Eggs were ground to a fine powder in a stainless steel mortar and pestle submerged in liquid nitrogen. Samples of the frozen powdered eggs were weighed while frozen and used in subsequent analysis.

Lipid samples were prepared for analysis by extracting about 1 g of the frozen, powdered eggs in 10 mL of 1:1 chloroform:methanol for 6 h on a mechanical shaker. Lipid extracts were separated into classes for positive identification on silica gel thin-layer chromatography (TLC) plates using a 90:10:1 petroleum ether:ethyl ether:acetic acid solvent system with comparison against known standards. Wax esters were differentiated from cholesterol esters, which have similar R_f values, by charring of the plates with H_2SO_4 and noting the presence or absence of the characteristic red color of the cholesterol moiety (Kates 1975).

After initial identification of lipid classes on TLC plates, subsequent separation and quantification was rapidly and efficiently carried out using a relatively new method, the Iatroscan TH-10 lipid scanner, which combines TLC with flame ionization detection (TLC–FID) (Kramer et al. 1980; Harvey and Patton 1981). In this system, individual samples were spotted on thin silica-covered rods (Chromarods®) which were placed in a solvent tank and separated by differential mobility as with standard TLC. After drying, rods were burned sequentially in a flame ionization detector and the amounts of different lipid classes were quantified. Lipid classes were separated using a 60:40:1 benzene:hexane:acetic acid solvent system. The samples were quantified by flame ionization detection and the output was recorded and integrated on a Hewlett-Packard 5840 integrator designed for gas chromatography. With this system, 10 samples could be separated and quantified in less than 30 min, consuming only 2 μL of each 10-mL extract. Total lipids were determined by focusing the lipids on Chromarods in a methanol solvent system, according to the method of Harvey and Patton (1981). For comparison, total lipid concentrations were also determined by the classic dry weight method (Bligh and Dyer 1959).

Samples for glycogen analysis were prepared by extracting about 100 mg of powdered tissue in 10 mL of boiling NaOH, deproteinated by ethanol precipitation, and determined colorimetrically by reaction with the Anthrone reagent according to methods developed for tissues of low glycogen content (Seifter et al. 1950). After ethanol precipitation of glycogen, protein concentrations were determined from the supernatant using the Lowry method. Dry weights were determined by lyophilization of unextracted eggs.

Methods for adenylate analysis are described in detail in Vetter and Hodson (1982). Briefly, the frozen egg powder was mixed with frozen powdered 6% perchloric acid. This mixture was allowed to thaw at 0°C in an ice bath. The perchloric acid infiltrates and denatures ATPases and other enzymes which would otherwise degrade ATP. The extracts were centrifuged and the protein pellet was removed to prevent reactivation of enzymes after neutralization. Once protected from enzymatic attack the adenine nucleotides are relatively stable. An aliquot of the egg extract was then neutralized with potassium carbonate, the precipitate was removed by centrifugation, and the sample was brought to a constant volume of 5 mL with Tris buffer (pH 7.4). ATP was measured directly using the luciferin–luciferase bioluminescence reaction in which light emitted is proportional to ATP concentration. The phosphorylated cofactor phosphoenolpyruvate and pyruvate kinase or pyruvate kinase plus myokinase were used to enzymatically convert ADP and AMP to ATP. Bioluminescence was quantified with a Science Application Industries SAI-3000 photometer. Conversion efficiencies of ADP and AMP to ATP were generally above 98 and 85%, respectively, and were corrected by using separate standard curves and regression equations for the three adenylates. Adenylate concentrations are expressed as nanomoles of adenylate per gram wet weight of eggs.

Results and Discussion

Lipid

Concentrations of the four lipid classes identified by TLC–FID, as well as total lipid concentrations, are reported in Table 1. Energy storage lipids (triglyceride and wax ester) and total lipid are reported in Fig. 1A. Total lipid concentrations based on the TLC–FID method of Harvey and Patton (1981) were slightly higher than but highly consistent with results of dry weight determinations. The increased speed of sample processing and reduced sample size are tremendous advantages of the TLC–FID method. This method also prevents volatilization of low molecular weight lipids during drying. Total lipids of red drum eggs decreased by 30% during the 17.5 h of development. Kaitaranta and Ackman (1981) surveyed the lipid content of roe from six species and found that total lipid content varied from 2.4% in the fastest developing species (Baltic herring, *Clupea harengus*, 2.5 wk) to 9.2% in the slowest developing species (rainbow trout, *Salmo gairdneri*, 20 wk). They suggested that lipid content may reflect the energy needs of different lengths of development. Assuming that our initial sample represents a condition similar to the unfertilized roe of red drum, the lipid content (2.4%) does reflect the short development time. However, it is impossible to directly relate lipid content to development time without knowledge of protein contribution to catabolism. For example, herring eggs (development time 2.5 wk) have about the same lipid content as red drum eggs (development time 22 h), but herring also rely on protein as an energy source (Eldridge et al. 1977). Decrease in lipid content during development was distributed among all four

TABLE 1. Concentration (mg/g wet wt ± 1 SD) of different lipid classes in developing red drum eggs 0.5, 4, 12, and 18 h after fertilization. Total lipid (as determined by TLC–FID) is expressed as the average and the range. Each sample weighed about 1 g and contained about 200 eggs from the same spawn (n = number of replicate samples).

Lipid class	n	0.5 h	4 h	12 h	18 h
Wax ester	5	6.81±0.53	6.01±0.38	5.92±0.35	4.68±0.49
Triglyceride	5	7.54±0.41	6.25±0.20	6.36±0.47	5.08±0.19
Cholesterol	5	1.50±0.17	1.16±0.10	1.17±0.08	0.71±0.16
Phospholipid	5	7.75±0.84	8.84±0.46	6.40±0.59	6.16±0.56
Total lipid (TLC–FID)	2	23.60±1.54	22.26±0.23	19.85±1.15	16.61±2.54
Total lipid (dry wt)	1	21.17	19.92	18.00	15.80

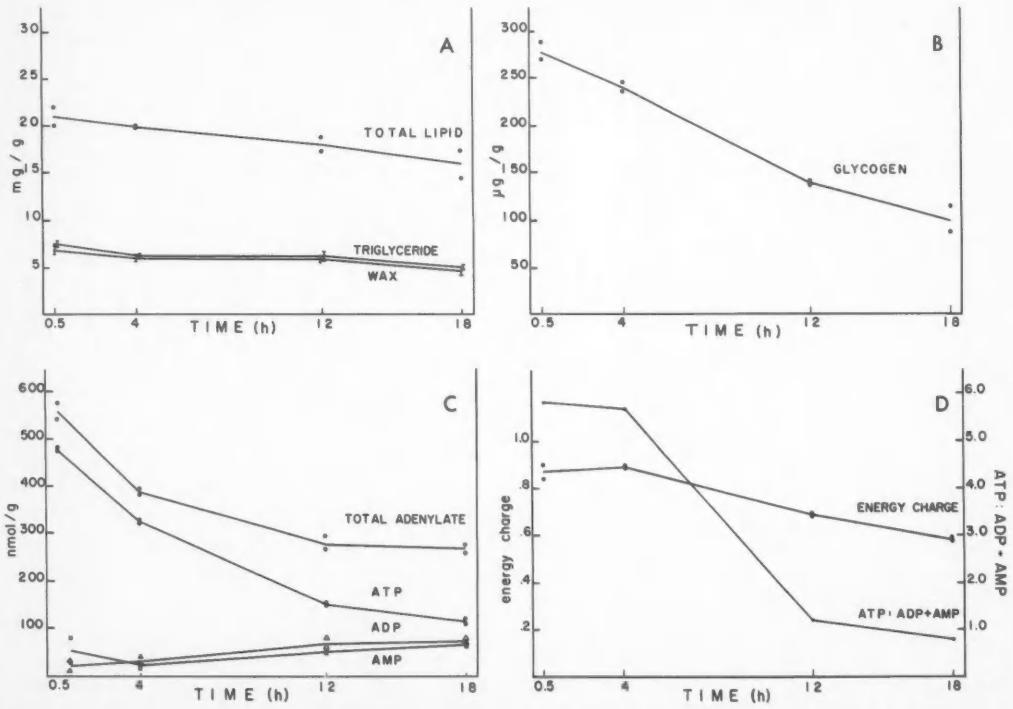

FIG. 1. Changes in energy reserves and adenylate ratios during 18 h between fertilization and hatching of *Sciaenops ocellata* eggs. (A) Changes in lipid reserves. Triglyceride and wax are given with ±1 SD limits at the four sampling times. All values are on a wet weight basis. (B) Changes in glycogen reserves. The line is drawn through the average values. Results are on a wet weight basis. (C) Changes in adenylate concentrations. The lines are drawn through the average values. Results are on a wet weight basis. (D) Changes in adenylate ratios during development.

lipid classes, and there appeared to be no sequential usage of triglyceride before wax ester as occurs in many marine organisms (Lee et al. 1974). Red drum eggs contained about 50% of their neutral lipid reserve in the form of wax ester. Although the occurrence of large deposits of wax ester in fish eggs has been previously reported, the reasons for its occurrence are still a matter of conjecture. The rapid development of red drum eggs would preclude the idea that it represents a long-term storage product, as is the case in copepods (Nevenzel 1970; Lee et al. 1974). Wax may aid in buoyancy regulation, since it is less dense than triglyceride.

GLYCOGEN AND PROTEIN

Glycogen has been shown to be the primary carbohydrate reserve in all fish eggs studied to date (see reviews by Terner

TABLE 2. Glycogen (mg glucose equivalents/g wet wt), protein (mg/g wet wt, assuming a water content of 930 mg/g), and water (mg/g wet wt) contents of red drum eggs during development 0.5, 4, 12, and 18 h after fertilization. Each sample weighed about 1 g and contained about 200 eggs from the same spawn (n = number of replicate samples). Results are expressed as the average and the range.

Compound		0.5 h	4 h	12 h	18 h
Glycogen	2	0.279±0.010	0.239±0.004	0.143±0.001	0.103±0.014
Protein	2	19.67±1.40	19.81±0.14	—[a]	24.40±0.46
Water	1	930.00	933.00	—[a]	925.00

[a]Insufficient sample for determination.

TABLE 3. Adenine nucleotide concentrations (nmol adenylate/g wet wt), total adenylates energy charge ratio and ATP: ADP + AMP ratio in developing red drum eggs 0.5, 4, 12, and 18 h after fertilization. Each sample weighed about 1 g and contained about 200 eggs from the same spawn (n = number of replicate samples). Results are expressed as the average and the range.

Compound	n	0.5 h	4 h	12 h	18 h
ATP	2	480±3	329±0.5	157±5	119±6
ADP	2	24±10	34±7	74±7	79±1
AMP	2	59±25	24±7	54±2	73±1
Total	2	564±18	386±2	285±14	271±8
Energy charge	2	0.87±0.03	0.89±0.01	0.68±0.01	0.58±0.01
ATP:ADP + AMP	1	5.78:1	5.67:1	1.23:1	0.78:1

(1979) and Boulekbache (1981)). The concentration of glycogen in the eggs of red drum decreased 63% throughout embryonic development (Table 2; Fig. 1B). Gluconeogenic processes, which do occur in fish eggs (Terner 1968; Milman and Yurowitsky 1973), could theoretically allow higher dependence on carbohydrate metabolism than predicted based on absolute changes in glycogen pool size. However, in terms of an overall energy budget, the major sources for de novo synthesis of carbohydrate by gluconeogenesis would be proteins, which did not decrease (Table 2), and glycerol from triglyceride metabolism, which is included in the lipid pool. We conclude that neutral lipid stores, which were almost always 100-fold greater than glycogen stores, are quantitatively the most important source of energy throughout egg development. In addition, only 37% of the initial glycogen reserve remains at the time of hatch, while 68% of the neutral lipid remains, suggesting that lipid is also quantitatively more important than glycogen during posthatch larval development. Although glycogen appears to be of lesser quantitative importance than neutral lipid, there is evidence that glycolysis is critical in certain phases of development, e.g. gastrulation in trout (Smith 1957; Boulekbache 1981). In addition, since lipid is unavailable under anaerobic conditions, glycogen may be critical for brief periods of environmental hypoxia. In red drum eggs, glycogen and lipid were used concurrently throughout development. While turnover of the protein pool undoubtedly occurred, the overall concentration of protein did not decrease during development, suggesting that protein is not an important energy source during egg development (Table 2).

ADENINE NUCLEOTIDES

The total concentration of adenylates and the concentration of ATP relative to its breakdown products, ADP and AMP, decreased in red drum eggs during embryonic development (Table 3; Fig. 1C). ATP concentration of the eggs decreased by 75% from fertilization to hatching. While ADP and AMP increased during this time, the loss of ATP was not stoichiometrically balanced by increases in ADP and AMP but resulted in a decrease in the total adenylate pool. This was probably the result of further breakdown of AMP to compounds such as inosine monophosphate (IMP). This allows EC to be maintained as ATP pools decrease (Chapman et al. 1976; Atkinson 1977). The adenylate EC ratio was maintained at about 0.88 during the first 4 h of development, while the total adenylate pool decreased by 32% (Table 1; Fig. 1D). After this period of stability, EC decreased to a low of 0.58 just prior to hatching. Since the adenine nucleotides are the principal compounds involved in energy transfer in cells, the relative concentrations of ATP, ADP, and AMP reflect the energy status of a cell and serve as allosteric feedback modifiers of such competing processes as glycolysis and gluconeogenesis (Atkinson 1977). Although this regulation is not completely understood, in general, high levels of ATP inhibit glycogenolysis and glycolysis and stimulate gluconeogenesis, while high levels of AMP stimulate glycolysis, the TCA cycle and the regeneration of ATP. The nature of adenylate regulation in teleost embryos may differ, since the egg must simultaneously maintain high rates of anabolism (in the case of red drum, producing a complete larval fish in about 24 h) and high rates of catabolism of stored reserves all in the absence of exogenous energy supplies. In red drum eggs, a continuous decline in ATP concentrations and EC would presumably allow glycogenolysis and lipid hydrolysis to proceed at maximum rates throughout embryonic development.

The turnover time of the ATP pool is on the order of seconds, and degradation of ATP by ATPases in samples can be extremely rapid. As Terner (1968, 1979) demonstrated, the way in which embryos are extracted for adenylate

determination can profoundly affect results. We believe that the liquid nitrogen protocol developed for this study is the most accurate available. Comparisons with the adenylate concentrations or EC's reported for other fish eggs should be made with caution, since many results are conflicting and older sample preparation methods may be inaccurate (e.g. Milman and Yurowitski 1973), and in some cases the methods are not reported (e.g. Boulekbache 1981). For the loach, Zotin et al. (1967) found a 30% decrease in ATP. Milman and Yurowitski (1973) found a stable adenylate concentration and a stable EC (0.73) throughout development, but reported a large drop in EC between oocyte (0.85, gluconeogenesis predominating) and fertilized embryo (0.74, glycogenolysis predominating). Boulekbache (1981) reported a range of EC's from 0.72 to 0.61 from fertilization to closure of blastopore in trout. Despite the variation in results, general conclusions from our and other studies appear to be that for teleost eggs, in general, EC's are lower than those of amphibian and mammalian embryos, often ranging below 0.80, a level indicating stress in many organisms. In addition, ATP concentrations appear to be greatest at fertilization and decrease during subsequent development.

An inability to attribute a clear regulatory role for changes in adenylate concentration and to reconcile high rates of anabolism with low adenylate ratios may originate from consideration of the egg as a homogeneous unit. Boulekbache (1981) measured lactate dehydrogenase (LDH) activity in the embryonic shield and enveloping layer of trout embryos and found large differences in LDH and presumably differences in aerobic and anaerobic metabolism. Although no one has reported adenylate concentrations from different areas of the developing embryo and yolk, it appears plausible that compartmentalization with different EC environments could allow anabolic and catabolic processes to operate at different rates in different areas of the egg under conventional adenylate regulation, which might be obscured by gross measurement of the entire egg.

Summary Discussion

This is the first study in which lipid, glycogen, protein, and adenine nucleotides were all measured concurrently during development of a teleost egg. The net energy contribution and percent change of different sources of energy are presented in Table 4. Protein is not included, since there was a net gain in protein concentration. The caloric contribution of an energy reserve was generally proportional to its absolute initial concentration and inversely related to its rate of decrease. Clearly, the two forms of neutral lipid reserves were quantitatively the most important source of energy throughout development despite their slow rate of decrease. Together they provided over 98% of the energy consumed during development. This energy budget approach also points out the fallacy of referring to ATP as an energy store rather than an energy transfer compound. Even with a 75% decrease in absolute ATP concentration it accounted for only 0.0025 cal/g (1 cal = 4.1868 J) or less than 0.01% of the measured energy consumed during development.

Attempting to determine which aspects of our results are unique to small rapidly developing eggs and which are the result of improved analytical techniques is extremely difficult, partly because of confusion in the existing literature. This is particularly true with regard to protein as an energy source. While earlier reviews (Needham 1931, 1942; Smith 1957) indicate that protein is perhaps the most important source of energy, the reviews of Williams (1967) and Blaxter (1969) leave open the question of protein catabolism, presenting studies that show large amounts of protein catabolism and others that show virtually none. The two most recent reviews of energy metabolism (Terner 1979; Boulekbache 1981) omit discussion of protein catabolism as a source of energy, yet they present no new papers that disprove earlier work. Direct determination of protein catabolism is extremely difficult because of the apparent reduced permeability of the chorion to nitrogenous wastes. Consequently, investigators have generally relied on indirect measurements (Lasker 1962; Williams 1967; Blaxter 1969). Despite the difficulty of measurement, protein catabolism should not be ignored in future studies. The apparent lack of protein catabolism in red drum eggs is similar to development in the medaka (*Oryzias latipes*) (Monroy et al. 1961) and amphibians (Williams 1967). There is also some evidence that development at warm temperatures, as occurs in red drum, may favor lipid metabolism over protein metabolism (Lovtrup 1959; Ehrlich and Muszynski 1982). The reliance on lipid as the primary energy source is reflected in the relative percent dry weight of lipid and protein. Flachter and Pandian (1968) have stated that the demersal egg contains 75% protein and 25% fat. Lasker found that the Pacific sardine was 70% protein and 12.7% fat. The ratio in red drum eggs was nearly 50% protein and 50% fat (dry weight). The amount of protein actually available for metabolism in small eggs may be considerably less, since the chorion takes on a proportionately greater significance due to surface to volume considerations. Blaxter and Hempel (1966) reported that 30% of the dry weight of Atlantic herring eggs was chorion; Eldridge et al. found 29% dry weight for the Pacific herring (1979).

The rate of development of red drum eggs is quite rapid relative to other better-studied species. However, this may be a function of the temperature of incubation rather than a

TABLE 4. Net decreases in different energy reserves during an 18-h period between fertilization and hatching in red drum (*Sciaenops ocellata*) eggs. Values expressed on a wet wt. basis.

Compound	% Original pool consumed	Amount consumed	Caloric value	Total caloric contribution
Triglyceride	31%	2.13 mg/g	9 cal/mg	19.17
Wax ester	33%	2.46 mg/g	9 cal/mg	22.14
Glycogen	63%	0.176 mg/g	4 cal/mg	0.704
ATP	75%	0.361 μMol/g	.007 cal/μMol	0.0025

unique metabolic adaptation. The review of Blaxter (1969) and the book by Russell (1976) present excellent summary graphs of the effect of temperature on development time; Russell (1976), in particular, presented data on small, buoyant pelagic eggs. Although the normal development temperature of red drum eggs (23–26°C) falls outside the limits of almost all the data presented, the development time is coincident with the predicted development times of most other species extrapolated to these higher temperatures. Thus, there appears to be no apparent metabolic adaptations for precocious development.

Buoyancy is a critical factor for the eggs of red drum and other estuarine species whose eggs commonly encounter waters of reduced salinity. Red drum eggs float at salinities above 25‰ and sink at salinities below it when spawned at 26–32‰. Percent hatch was decreased at low salinity due to crowding, fungal infection, and low oxygen, all associated with sinking and crowding rather than salinity effects per se (Holt et al. 1981a). A similar pattern occurs with the spotted seatrout (*Cynoscion nebulosus*) and the common sole (*Solea solea*) (Fonds 1979). The role of lipid, particularly wax ester, in maintaining buoyancy at low salinities deserves further consideration. Fishes are routinely grouped into freshwater or marine species, with the former producing demersal eggs and pelagic members of the latter group producing small buoyant eggs. Based on this grouping, buoyancy as a principal function of lipid has at times been discounted, since many pelagic eggs do not contain oil droplets (Smith 1957; Russell 1976) and there is ample evidence for osmoregulatory control of buoyancy in a hypertonic medium such as seawater (Solemdal 1967; Blaxter 1969). However, estuarine-dependent species such as the red drum are in the difficult situation of producing small buoyant eggs often in waters of low salinity where the specific gravity and hence the lifting power of the medium is less and where the egg is sometimes hypertonic to the surrounding medium. Under these conditions, osmoregulatory control of buoyancy would be more difficult. The occurrence of marine waxes and their possible functions have been reviewed (Sargent et al. 1976; Sargent 1978). The studies noted that the specific gravity of triglyceride is 0.92 and of wax esters is 0.86 at 21°C. In seawater (specific gravity 1.026), wax would contribute 70% more upthrust per unit volume. Large quantities of wax ester have been found in the eggs of red drum, spotted seatrout, striped mullet (*Mugil cephalus*), gouramis (*Trichogaster cosby*) (Nevenzel 1970), perch (*Perca flaviatilis*), and burbot (*Lota lota*) (Kaitaranta and Ackman 1981). All of the above species, except the gouramis, produce eggs and larvae that commonly encounter reduced salinities. The gouramis is one of the few freshwater species that produces buoyant eggs (Goldstein 1971).

The significance of adenine nucleotide changes during red drum development is impossible to fully evaluate at this time. Regardless of the validity of the energy charge concept, which is certainly open to question, there is no doubt that many metabolic regulatory enzymes respond allosterically to the levels of different adenine nucleotides. The continual decline of ATP may indicate an inability of ATP production to keep pace with ATP demand and would presumably stimulate rates of catabolism of the yolk and oil droplet until a maximum rate is reached. Some studies have attempted more precise interpretation of adenylate changes and their effect on energy stores (Boulekbache 1981). However, it must be established that the rates of consumption of different reserves are not maximum rates, or they are outside the limits of normal adenylate regulation. In addition, our understanding of adenylate regulation is still rudimentary and study has focused primarily on the glycolytic pathway rather than the regulation of protein transamination reactions or β-oxidation of fatty acids. Since simple metabolism of carbohydrate was not a significant source of energy in these eggs, the complete significance of changes in adenine nucleotides must await advances in our understanding of basic cell regulation.

Conclusions

The eggs of red drum are representative of many warm-water estuarine species which produce small, buoyant pelagic eggs which develop rapidly in waters of reduced salinity. The extremely rapid rate of development appears to be a function of temperature effects on metabolism rather than a unique adaptation to precocious development. The eggs rely almost entirely on lipid rather than protein or carbohydrate for the catabolic energy of development. Glycogen, triglyceride, and wax ester were used concurrently rather than sequentially during development. The presence of large reserves of lipid in the form of wax ester may provide buoyancy as well as energy in small eggs developing in low-salinity waters where osmoregulation alone may be insufficient for buoyancy. Decreases in ATP concentrations indicate that energy synthesis does not keep pace with energy demands and that catabolism of energy reserves may be proceeding at maximum rates.

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NOTES

Redundancy of Variables Used to Describe Importance of Prey Species in Fish Diets

J. STEVENSON MACDONALD[1] AND R. H. GREEN

Department of Zoology, University of Western Ontario, London, Ont. N6A 5B7

MACDONALD, J. S., AND R. H. GREEN. 1983. Redundancy of variables used to describe importance of prey species in fish diets. Can. J. Fish. Aquat. Sci. 40: 635 – 637.

Information redundancy associated with three measurement variables were examined using food habit data from five species of demersal fish in the lower Bay of Fundy. Number, weight, and percent frequency of occurrence measures of three prey species all load heavily on the first principal component of a PCA and are therefore highly correlated. We conclude that it is probably not necessary to create compound indices of prey species importance when documenting soft-bottom benthic associations or demersal fish food habits. Compound indices add little new information when compared with any single measure.

MACDONALD, J. S., AND R. H. GREEN. 1983. Redundancy of variables used to describe importance of prey species in fish diets. Can. J. Fish. Aquat. Sci. 40: 635 – 637.

Les moeurs alimentaires de cinq espèces de poissons démersaux de la portion inférieure de la baie de Fundy ont servi à étudier le volume excessif de données avec trois variables de mesures. Les nombres, poids et pourcentage d'occurrence de trois espèces proies sont tous des données qui influencent fortement la première composante principale d'une analyse en composantes principales (PCA) et sont donc en étroite corrélation. Nous concluons qu'il n'est probablement pas nécessaire de créer des indices composés d'importance d'espèces proies quand on veut démontrer des associations benthiques de fonds mous ou les moeurs alimentaires de poissons démersaux. Ces indices ne donneraient que peu d'informations nouvelles comparés à toute mesure unique.

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IN an effort to identify dominant or important prey species researchers of animal diet have used several types of measurements. They include numerical abundance, volumes or weights, percent frequency of occurrence, and energy value (reviewed by Hynes 1950; Berg 1979; Hyslop 1980). Each measure was developed to fulfill a different purpose. Numerical abundance measures reflect the process of density-dependent prey acquisition by predators and thus provide insight into feeding behavior. They may have an advantage if weight cannot be obtained (as on a research vessel) or if the researcher wants to avoid the problem of back-calculating original weights or volumes from taxonomic measures of digested prey (Windell and Bowen 1978). Volume or weight measures reflect prey species nutritional value and should be used when prey species are too numerous to be counted (Richards 1963). Ellison (1978) has noted the importance of using actual energy value as a measure of importance. Energy values were not available for the prey species in this study. Percent frequency of occurrence gives an indication of prey species variability in predator diets. Frost (1977) has found percent occurrence measures to be particularly appropriate when there are few food categories.

Researchers have assumed that such different measurement types contain substantial independent information (Hyslop 1980). To avoid information loss several methods have been developed to combine two or more measures. Hynes (1950 — points method) and Hureau (1969 — in Berg 1979) create indices that combine numerical and volumetric measures. Pinkas et al. (1971) and Prince (1975) combine percent numbers, volumes, and occurrence (index of relative importance — IRI). These indices are based on an equal contribution by each type of measure. Cailliet (1976), Hulberg and Oliver (1978) and Hacunda (1981) have used Pinkas' IRI. Cailliet, Hulberg and Oliver use abundance, volume, and percent frequency of occurrence measurements type to define rectangles which are compared among prey species and among predator species.

Compound indices are not exclusive to dietary research. Numbers and weight have been used to describe numerically dominant species in marine benthic samples by Ellis and Conlan (1979). Curtis and McIntosh (1951) combine density, frequency and dominance estimates to measure plant species importance in an upland forest in Wisconsin.

This note addresses the question of data redundancy that may occur among abundance, volume, and percent frequency of occurrence measurements. It may not be necessary to combine all measures into one index if one measure describes most of the information.

[1]Present address: Department of Fisheries and Oceans, West Vancouver Laboratory, 4160 Marine Dr., West Vancouver, B.C. V7V 1N6.

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TABLE 1. Transformations required by each variable type for each invertebrate species to remove the variance associated with the mean.

Prey	*Ninoe nigripes*	*Leptocheirus pinguis*	*Yoldia sapotilla*
Transformations	No. $Z = X$ Wt. $Z = X^{0.8694}$ Occ $\theta = \arcsin X$	$Z = \ln(X + 1)$ $Z = X^{0.285}$ $\theta = \arcsin X$	$Z = \ln(X + 1)$ $Z = X$ $\theta = \arcsin X$

Materials and methods — Data were collected as part of a study of spatial and temporal variation in fish diet in the lower Bay of Fundy region, N.B., Canada (45°N, 67°W). Three hundred and ninety-seven stomachs from five species of fish (*Pseudopleuronectes americanus* — winter flounder, *Hippoglossoides platessoides* — American plaice, *Gadus morhua* — Atlantic cod, *Macrozoarces americanus* — ocean pout, and *Glyptocephalus cynoglossus* — witch flounder) were collected from two sites at seven times over 1 yr (1979–80). Stomachs were removed immediately after capture and immersed in 10% formalin. They were later transferred to 70% ethanol. For 217 prey species identified, the numbers and blotted wet weights of each prey in each stomach were recorded and stored. Mean number, mean weight, and percent occurrence of three prey species (*Ninoe nigripes* — polychaete, *Leptocheirus pinguis* — amphipod, *Yoldia sapotilla* — bivalve) were calculated for each fish species caught at each site and time. The numbers and weights were transformed according to Taylor's power law (Elliott 1977; Tukey 1957) to remove the dependency of the variance on the mean. The percent occurrence data were treated using an arcsine transformation for the same reason (Sokal and Rohlf 1973). The transformed data were analyzed separately for each prey species using principal component analysis (FACTOR-SPSS; Kim 1975) to determine the amount of variation in the data that was shared among the measurement variables. This process was repeated after removal of the added correlation caused by cases (fish at each site and time) where all three measures were zero.

TABLE 2. Amount of variation accounted for by the first principal component of the analysis on each species. Runs were made with and without the added correlation caused by cases where all three measures were zero.

Prey		*Ninoe nigripes*	*Leptocheirus pinguis*	*Yoldia sapotilla*
Percent variation associated with first PC	All groups	95.5%	95.5%	90.5%
	No zeros	91.4%	91.4%	89.0%

Results — Numerical abundance data required either a square root or a log $(X + 1)$ transformation. This is consistent with the literature (Marriott 1974; Green 1979). Transformations for weight data were less predictable as each prey species required a different treatment under Taylor's power law (Table 1). The first principal (PC) component described a large portion of the variation whether or not groups with zero values were included (Table 2). All three measurement variables loaded heavily on the first principal component axis and were highly correlated with each other (Table 3).

Discussion — It is often desirable to reduce numbers of variables (see discussion in Green 1979). Large numbers of variables require extra work to collect and analyze, and they increase sensitivity to violations of assumptions in multivariate analyses. In many cases the additional information gained decreases rapidly as more variables are included (Kaesler et al. 1974). The high positive loadings on the first PC demonstrate that the three variables in this study are highly correlated and any one will adequately describe prey species importance regardless of the definition of importance. Compound indices are difficult to interpret and analyze statistically and do not increase the amount of information gained (Green 1979).

These results apply to any study where compound indices calculated from correlated variables might be used. In studies where determination of production and biomass is the objec-

TABLE 3. Variable loadings on the first three principal components of each species. Correlation coefficients associated with each species are also included.

		Ninoe nigripes			*Leptocheirus pinguis*			*Yoldia sapotilla*		
Prey		PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Correlation coefficients (loadings)	No.	0.986	−0.042	−0.163	0.975	−0.220	0.043	0.986	−0.111	−0.124
	Wt.	0.970	0.240	0.058	0.996	−0.055	−0.063	0.956	−0.278	0.098
	Occ.	0.976	−0.192	0.107	0.960	0.281	0.021	0.910	0.413	0.032
Correlation matrices (with zeros in data)		No.	Wt.	Occ.	No.	Wt.	Occ.	No.	Wt.	Occ.
	No.	1	0	0	1	0	0	1	0	0
	Wt.	0.937	1	0	0.981	1	0	0.961	1	0
	Occ.	0.952	0.907	1	0.857	0.939	1	0.847	0.758	1

tive, and prey sizes vary greatly, the choice of abundance versus weight measures will influence the results. For example, if a fish species consumes large and small prey, weight measurements will favor the large items. Variation of sizes of prey, in the diets of demersal fishes in the lower Bay of Fundy, is not large enough to create this problem. We expect our results to apply to diet measures of many freshwater and pelagic fishes. Before collecting abundance, weight *and* percent frequency of occurrence measurements researchers should analyze preliminary samples to determine the degree of shared information among the measurements.

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A Modified Freeze-Core Technique to Quantify the Depth Distribution of Fauna in Stony Streambeds

C. W. PUGSLEY AND H. B. N. HYNES

Department of Biology, University of Waterloo, Waterloo, Ont. N2L 3G1

PUGSLEY, C. W., AND H. B. N. HYNES. 1983. A modified freeze-core technique to quantify the depth distribution of fauna in stony streambeds. Can. J. Fish. Aquat. Sci. 40: 637–643.

A freeze-coring device using liquid nitrogen is described, which enables one person to take a columnar core, extending from the surface to at least 50 cm below a stony streambed. An experiment to validate the technique showed that animals did not flee from the advance of the freezing-front. Using frozen streambed cores, the vertical distribution of benthic invertebrates of two streams in southern Ontario was investigated. In contrast to previous estimates, ~ 70% of the fauna was found in the top 10 cm of the streambed, and invertebrate densities were often lower by an order of magnitude. These differences are attributed to problems of quantifying previous sampling methods.

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L'article qui suit contient une description d'un dispositif de carrottage-congélation à l'aide d'azote liquide permettant à une personne de prélever une carotte columnaire depuis la surface jusqu'à au moins 50 cm au-dessous du lit pierreux d'un cours d'eau. Lors d'une expérience menée en vue de vérifier la méthode, on a constaté que les animaux ne s'enfuyaient pas devant le front de congélation. De telles carottes congelées ont été prélevées dans une étude de la distribution verticale des invertébrés benthiques de deux cours d'eau du sud de l'Ontario. Contrairement aux estimations antérieures, on a trouvé qu'environ 70 % de la faune se trouvaient dans les 10 cm supérieurs du lit des cours d'eau et que la densité de ces organismes était souvent inférieure d'un ordre de grandeur. On attribue ces différences à des problèmes de quantification dans les méthodes d'échantillonnage antérieures.

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THREE main types of field sampling methods have been used to quantify the animals that live below a streambed; pumping, substrate colonization, and coring. Pumping is a commonly used method, and involves filtering measured quantities of interstitial water, pumped either from a standpipe driven to the required depth (Bou 1974), or from a multilevel piezometer (Husmann 1971).

To overcome problems of quantifying these pumped samples (e.g. selectivity against tenacious animals, volume and location of substrate sampled), a wide range of substrate colonization methods has been developed (Coleman and Hynes 1970; Bishop 1973; Hynes 1974; Poole and Stewart 1975; Gilpin and Brusven 1976; Morris and Brooker 1979). However, in addition to the usual criticisms which apply to substrate colonization (Rosenberg and Resh 1982), many of the samplers produce an additional bias by providing 'open corridors' to the deeper parts of the substrate (Coleman and Hynes 1970; Hynes 1974). This problem can be reduced by burying isolated 'colonization pots' in the streambed (Hynes 1974).

Of the three methods for sampling streambed fauna, coring is undoubtedly the best quantitative method available. Although corers used by Bretschko (1981), Ferencz (1968), and Sterba and Holzer (1977) appear difficult to use in stony substrates, the Williams corer (Williams and Hynes 1974) was designed for cobble–boulder streambeds and can be used to sample down to depths of 70 cm with relative ease. However, some doubt has been expressed about the accuracy of the quantitative data obtained with the Williams corer (Exner and Davies 1979; Williams and Hynes 1979; Williams 1981).

Freeze-cores seem to overcome some of the criticisms leveled at the Williams corer; i.e. substrate and fauna can be sampled simultaneously from both the surface and hyporheic zone. Shapiro (1958) and Efford (1960) used freezing techniques to sample benthos of shallow, cobble-free streambeds or mud lakebeds. Since then the main use of stream freeze-coring has been to characterize the substrate, particularly in fisheries work. A variety of methods using different coolants has been devised: solid carbon dioxide, with alcohol or acetone (Shapiro 1958); liquid oxygen (Efford 1960); liquid nitrogen (Stocker and Williams 1972), and liquid carbon dioxide (Lotspeich and Reid 1980; Carling and Reader 1981).

The paucity of fauna in freeze-cores taken by Stocker and Williams (1972) was attributed to the movement of animals away from the freezing front as it passed through the substrate. In the present study the validity of this hypothesis was tested before the technique was used to quantify the vertical distribution of benthic stream fauna. Stream colonization cages were frozen in the laboratory, so that the effect of freezing on the movement of invertebrates away from the freezing-front could be determined.

Methods — Validation of the freeze-core technique — Ten stream colonization cages (40 × 10 × 20 cm deep) were made from 2.5-cm wire mesh. Each cage was lined with 1 mm Nitex and fitted with a stoppered vertical pipe at one end. After filling with natural substrate, the lids were wired down and the cages buried below the streambed in a trench dug in Salem Creek, Ontario, at the site used by Godbout and Hynes (1982). After 4 wk in the stream (November–December 1980), the cages were lifted from the water and placed in wooden boxes insulated with polystyrene, and lined with a polythene bag to keep the substrate full of water.

Boxes were held at ambient stream temperature before freezing. Liquid nitrogen was passed into the vertical pipe located at one end of the box until the substrate was completely frozen. Temperature was indicated by a series of thermometers embedded in the substrate, which showed that the temperature plunged to at least −30°C in a fraction of a second once the freezing-front reached the thermometer. After freezing was complete, each box was thawed while inverted over four 10-cm-wide Plexiglas compartments, each containing 4% formalin. With the substrate now divided into four equal parts across the width of the colonization cage, animals were separated by elutriation (Stewart 1975), and larger shells and cases hand-picked. Elutriated material was passed through a 160-μm mesh, stored in 70% ethyl alcohol, and stained with rose bengal (100 $mg \cdot L^{-1}$). After flotation in saturated calcium chloride, the animals were sorted into major taxonomic groups and counted. Faunal densities were calculated in each of the four (10 × 10 × 20 cm) sections of the

colonization cages; i.e. at a mean distance of 5, 15, 25, and 35 cm away from the freeze pipe.

Bartlett's Test for homogeneity of variance demonstrated that faunal density among the four sections was homogenous ($B_c = 1.18$; df = 3; $0.75 < P < 0.9$). A single factor analysis of variance showed that there was no significant difference in the density of the fauna in the four sections of the cages after freezing ($F = 0.30$; $P = 0.83$). It was therefore concluded that there was no migration of invertebrates away from the freezing-front as it moved along the length of the colonization cage. Stocker and Williams (1972) did find animals in their freeze-cores but "significantly fewer" than the number collected using "two other techniques." Using their technique the upper 10 cm of core was incomplete. This, combined with perhaps an expectation of large faunal densities at depth may have led them to the rejection of the freeze-core as a method of quantifying streambed fauna.

There seems no reason to think that the freezing-front advances any more slowly in the field than it does in the laboratory validation experiments. Therefore, based on these results, the liquid nitrogen freeze-core technique used by Stocker and Williams (1972) was chosen for modification. The low-pressure delivery system; the cost, availability, and low temperature of the coolant; and the cheap, simple, robust design of the standpipe were the features which favored the selection of this particular freezing method over the many available.

Design and operation of the modified freeze-core sampler — The standpipe (Fig. 1) is almost identical with that used by Stocker and Williams (1972). The small nodules of weld around the base, which help secure the frozen core to the pipe during extraction from the streambed, and the two welded rings have been retained. However, the diameter of the standpipe has been increased to 35 mm (ID) and a single strip of adhesive tape replaces the 10-cm marked grooves as a depth marker. A heavier 10-kg pounder with side handles and a 60-cm long sleeve was used to drive standpipes into the streambed at least 48 h before freezing the core, thereby allowing faunal distributions to recover from the vibrations and disturbance.

The steel cap used to protect the top of the standpipe while it is being driven into the streambed is vital, as any distortion of the untoughened (4 mm wall thickness) steel water-pipe would prevent the brass fitting for the liquid nitrogen outlet ports from being lowered down the inside of the standpipe. To keep water from entering the standpipe before freezing, the weld securing its conical drive tip must be water-tight, and, if rain is expected, rubber stoppers are needed to seal the holes where the steel pin is to be inserted.

To freeze a cylindrical core from the surface of the streambed to a depth of 50 cm takes about 20 min and consumes about 10 L of liquid nitrogen. The procedure begins with the removal of all rubber stoppers from the standpipe, the clearing of any large boulders from around the base, and the attaching of one or more styrofoam insulators with rubber bands to the submerged part of the pipe. Insulators must contact the substrate to reduce the heating effect of streamflow or else the top 10 cm of the core may not be frozen successfully. A streamflow deflector plate is also necessary in warm, fast-flowing

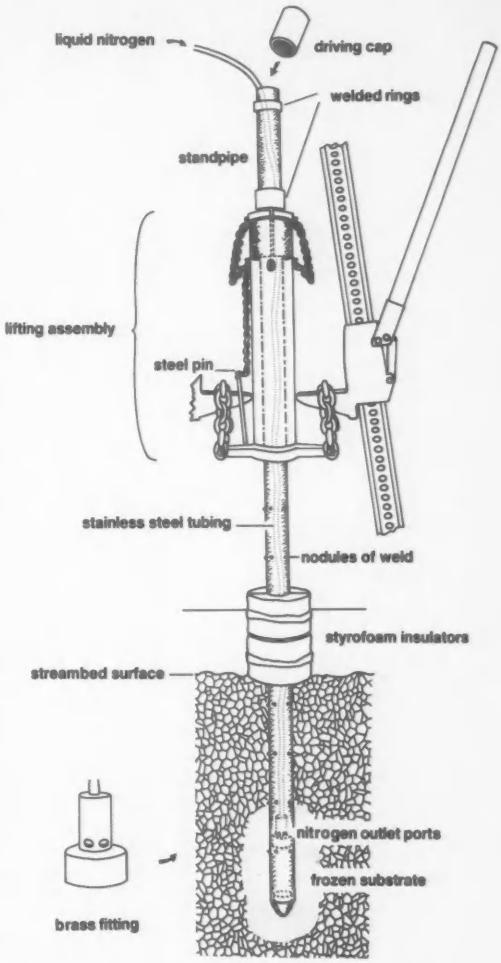

FIG. 1. Freeze-core equipment being used to sample a stony streambed.

streams. The lifting assembly is lowered over the standpipe, and the two steel split rings are dropped in place. The toughened 12-mm diameter stainless steel pin is inserted, securing the lifting assembly to the standpipe. Two truck jacks are attached to the stout lifting chains. Once in place they hold the lifting assembly, so that the steel pin can be removed, and the liquid nitrogen delivery system set up.

A robust Dewar flask (20 L), equipped with a pressure gauge and emergency pressure relief system, is set on a table in the stream. A 2-m length of flexible stainless steel tubing (7 mm, ID) is lowered down the inside of the standpipe. The brass fitting (32.5 mm diam) on the end is a close fit to ensure that liquid nitrogen from the four 6-mm-diameter outlet ports

TABLE 1. Summary of studies on the quantity and vertical distribution of stream benthos.

Location of sampling site and reference.	Sampler type; mesh size (μm), sampling depth (cm), time of year when samples collected.	Invertebrates in 1 m^2 of streambed ($\times 10^3$). (n = no. of samples from each depth interval.)	Percentage of fauna found at depth in the substrate (depth ranges in cm.)
	Speed River		
Speed R., southern Ontario (This study).	Freeze corer, 160, 50, throughout year.	42 (n = 14)	21% (10–50) 6% (20–50)
Speed R. (Coleman and Hynes 1970).	Substrate colonization, 170, 30, June and July.	281 (n = 16)	80% (8–30) 53% (15–30)
Speed R. (Hynes 1974).	Substrate colonization, (superpots), 170, 54, throughout year.	94 (n = 29)	14% (13.5–54)
Speed R. (Williams and Hynes 1974).	Williams corer and kick sampler, 100, 75, throughout year.	619 (n = 60)	97% (5–75) 62% (15–75)
	Salem Creek		
Salem Ck., southern Ontario (This study).	Freeze corer, 160, 50, July and Aug.	94 (n = 4)	34% (10–50) 10% (20–50)
Salem Ck. (Godbout and Hynes 1982).	Williams corer, 110, and Surber sampler, 235, 65, June and Oct.	110 (n = 27)	77% (5–65) 41% (15–65)
	Other studies		
Kirkland Ck., southern Ontario (Williams and Hynes 1976).	Williams corer and kick sampler, 130, 65, May, June, Oct., Nov.	229 (n = 8)	93% (5–65) 49% (15–65)
Afon Hirnant, Wales (Hynes et al. 1976).	Williams corer and kick sampler, 130, 25, June.	323 (n = 12)	91% (5–25) 36% (15–25)
Theiss R., Hungary (Ferencz 1968).	Mechanical corer, 35 cm, October.	9 (n = 2)	8% (10–35)
Morava – Chomoutov. (a) Váh – Ratnovce. (b) Váh – N. Mesto. (c) Dunaj – Vojka. (d) Rudava – Studienka. (e) Czechoslovakia (Sterba and Holzer 1977).	Stovepipe type corer with grab to extract sediments, 100/130 cm, (a) throughout year (b) May, Oct., and Nov. (c) July and Nov. (d) Oct. and Nov. (e) July, Aug. and Oct.	(a) 25 (n = 11) (b) 35 (n = 7) (c) 41 (n = 2) (d) 44 (n = 3) (e) 1 (n = 3) mean 29 (n = 26)	59% (10–100) 63% (10–100) 76% (10–100) 85% (10–130) 28% (10–100) 62%
(a) a small creek, B.C. (b) spawning channel, B.C. (Mundie 1971).	Modified Hess type sampler, 50 15–30, April and July.	(a) 32 (n = 3) (b) 57 (n = 1)	26% (10–15/30) 41% (10–15/30)
Spawning channel (Gilpin and Brusven 1976).	Substrate colonization, 30 cm.	39 (n = 6)	21% (10–30)
Brazos R., Texas (Poole and Stewart 1976).	Substrate colonization, 500, 40, throughout year.	13 (n = 15)	34% (10–40)
Wye R., Wales (Morris and Brooker 1979).	Substrate colonization, 440, 33, June to Sept.	13 (n = 27)	41% (11–33)
Sungai Gombak, Malaysia (Bishop 1973).	Substrate colonization, 90, 40 throughout year.	10 (n = 5)	66% (10–40)

does not build up at the bottom of the standpipe. Starting with the outlet at the bottom, a constant flow of liquid nitrogen is maintained by regulating the pressure inside the Dewar flask, using nitrogen gas from a small gas cylinder. At 2-min intervals the delivery tube is lifted 10 cm, the position of the outlet being marked by adhesive tape at regular intervals on the tube.

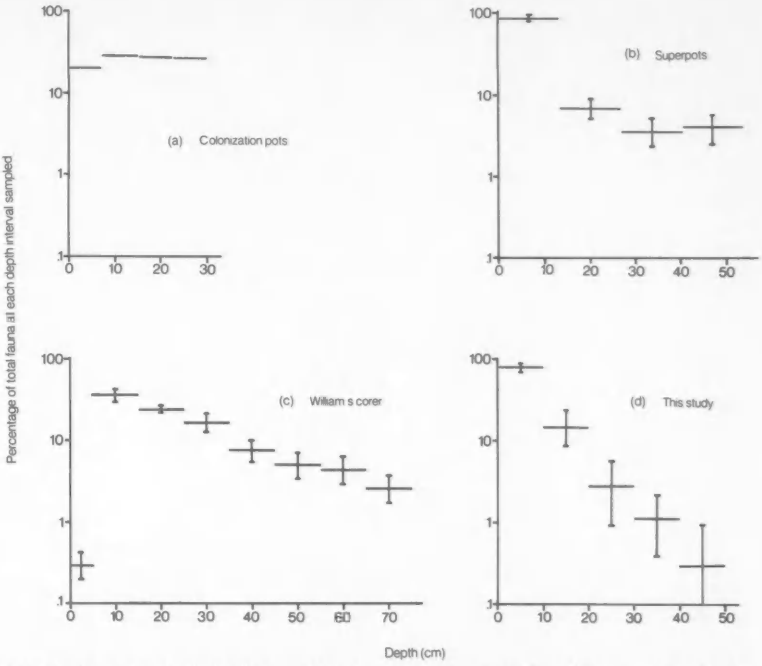

FIG. 2. Percentage depth distribution of benthic invertebrates in the Speed River, southern Ontario: (a) data from Coleman and Hynes (1970), summer 1966, substrate colonization pots, $n = 14$; (b) Hynes (1974) and unpublished data, samples throughout the year 1969–71, substrate colonization superpots, $n = 29$; (c) data from Williams and Hynes (1974), samples throughout the year 1970–71, Williams corer, $n = 60$ (Values taken from table 2 monthly means of five replicates so for confidence limits $n = 12$); (d) this study, samples throughout the year 1981–82, Speed River freeze-cores, $n = 14$. Mean values ± 95% confidence limits calculated after arcsine transformation of the data. n = the number of samples from each depth interval sampled.

An additional minute of freezing time is often needed near the surface of the streambed, after which the nitrogen outlet is lowered to the bottom of the standpipe for a final 2-min period, to secure the bottom of the core more firmly.

After freezing, the Dewar flask, nitrogen gas cylinder, and table are removed and the steel pin is inserted to prevent the jacks from rotating. The core can be raised by only one person operating each jack in turn; speed is essential, especially in summer. Considerable force is exerted by the jacks sufficient to shear boulders protruding from the core. Cores obtained with this method are cylindrical over the entire depth range and do not taper or form a tear-drop-shaped core e.g. Stocker and Williams (1972), Carling and Reader (1981). The diameter of the core is dependent on several factors, especially the temperature and flow of both surface and groundwater. In summer, with surface streamflow above 20°C, columnar-shaped cores of 10 cm diameter (ignoring exposed cobbles and boulders) were obtained. In winter, larger cores (15 cm diam) were obtained. The frozen cores were transported to the laboratory in insulated boxes containing dry ice or, if air temperatures were sufficiently high, thawed at the stream bank.

Before thawing, cores were photographed in color to measure core diameter and to identify layering of the substrate. They were then separated into 10-cm-vertical intervals by thawing over five Plexiglas compartments containing 4% formalin. These samples were stored and the fauna separated from the substrate as already described.

This freeze-core technique was used to determine the vertical distribution of benthos in stony streambeds, at sites on the Speed R. and Salem Creek previously sampled with colonization pots and the Williams corer (Table 1).

Results and discussion — Quantity and distribution of the fauna in the Speed R. and Salem Ck. — Most of the invertebrates sampled in this study were present in the upper 20 cm of the streambed (Fig. 2d). This result is not in accord with previous work using the Williams corer (Fig. 2c) or colonization pots (Fig. 2a) at the same sampling sites (See also Table 1), although the superpots (Hynes 1974) gave a similar result (Fig. 2b) in the Speed R. The number of invertebrates was also much lower than previously reported, although again there was a close agreement with the Speed R. superpots (Table 1).

However, direct comparisons of the hyporheic component are difficult when different depth intervals are used. This becomes critical when comparing the Williams corer with the other methods used (Table 1) as the uppermost sample is taken from −5 to −15 cm, and supplemented with a 0 to −5 cm Surber or kick sample (Williams and Hynes 1974). Freeze-core samples show there is a rapid decrease in faunal density with increasing depth. Therefore, the difference of 5 cm in the depth interval sampled using the freeze-cores and Williams corer may contribute to differences in the depth profile of animals found in the substrate.

Regardless of sampling technique, any discussion of differences in the vertical distribution of the fauna also depends on how the surface of the streambed is defined. In this study, the surface was taken as the level at which the substrate became consolidated, i.e. loose cobbles and boulders were removed before the freeze-cores were taken. Designating the zero point with a precision of more than ±2.5 cm is considered to be unrealistic. A Williams corer has to be driven repeatedly to get a complete depth profile. Therefore, changes in the zero point will also cause inconsistent sampling errors at the upper and lower margin of each 10-cm depth interval.

Another problem in comparing depth distributions is that the division into surface and hyporheic biotopes is somewhat arbitrary. In compiling Table 1, a depth of 10 cm has been used whenever possible as the dividing line for calculating the hyporheic component. An alternative approach would be to avoid this type of classification and consider the whole area beneath the surface of the streambed as a three-dimensional groundwater habitat.

Variations in density and vertical distribution of fauna — A survey of other quantitative studies is given (Table 1). If the original colonization pots used by Coleman and Hynes (1970) and the Williams corer are excluded, numbers of invertebrates found range from 1000 to 100 000 m^{-2}, most of which occur in the upper 10 cm of the streambed. In contrast, the Williams corer and the earlier type of colonization pots give values of between 100 000 and 600 000 m^{-2} with a much higher proportion of the fauna deeper down in the streambed (Table 1).

The freeze-core technique allows absolute in situ sampling of stream invertebrates simultaneously from the surface and deeper parts of a stony streambed, thus avoiding the problem of taking a separate sample for each depth interval. The area of substrate sampled can be measured from the core and, therefore, the density (no. m^{-2} or no. m^{-3}) of the fauna can be calculated directly. Although there is little disturbance to the streambed before the samples are taken, once the core has been extracted the habitat is destroyed. This, together with transporting the heavy, cumbersome equipment, and the limited number of cores that can be taken restrict the versatility of freeze-core sampling.

However, in contrast to the Williams corer, there is no bias towards sampling only the invertebrates associated with the smaller particle sizes (Williams 1981). Cobbles up to 15 cm in diameter were extracted with the freeze-core. In addition, the volume of a frozen core at each 10-cm depth interval was from 25 to 60 times that of the 25 cm^3 version of the Williams corer. This increased the number of animals collected at each depth and reduced reliance on counts of less than 10 animals at the deeper levels of the substrate. For example, the mean number of animals in a single 25 cm^3 capacity Williams corer sampled from depths below 35 cm was only 7 but this still represented 20% of the total fauna (Fig. 2c) or 123 800 animals · m^{-2} (Table 1 — data from Table 2, Williams and Hynes 1974).

The low numbers of animals in each sample and the chance that some of these become entrained with the corer as it is being driven into the substrate could explain why the Williams corer overestimates the hyporheic component and therefore invertebrate densities.

The slope of the curve relating faunal density with depth below the streambed is much shallower using Williams corer than it is for freeze-cores (Fig. 2 c, d). A shallow slope may be predicted if entrainment of surface fauna occurs, with fewer animals being carried by the corer to the deeper levels. Placing the freeze-core standpipe in the streambed several days before freezing removes the problem of errors caused by entrainment.

We still consider the Williams corer to be a useful sampling tool for the hyporheos. However, if quantitative information is needed, the freeze-core technique is probably more accurate. The lack of any clear relationship between faunal density and depth using colonization samplers (Fig 2a) is probably an artifact, emphasizing the problem of quantifying results obtained in this way.

The considerable variation in both the vertical distribution and density of stream invertebrates shown by Table 1 demonstrates the inherent variability of the stream habitat as well as systematic errors in sampling. Reliable sampling is the key to solving many ecological questions. The freeze-core method offers a means of collecting absolute samples of stream invertebrates. A freeze-core also gives an excellent sample of the substrate taken with the animals. The three-dimensional distribution of fauna and their relationship with the substrate will be dealt with in a later paper.

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Taxonomy of a Swimbladder Nematode, *Cystidicola stigmatura* (Leidy), and Evidence of its Decline in the Great Lakes

GEOFF A. BLACK

Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ont. N1G 2W1

BLACK, G. A. 1983. Taxonomy of a swimbladder nematode, *Cystidicola stigmatura* (Leidy), and evidence of its decline in the Great Lakes. Can. J. Fish. Aquat. Sci. 40: 643 – 647.

Cystidicola stigmatura (Leidy, 1886) Ward and Magath, 1917 is considered a valid species after examination of specimens from Leidy's collection. *Cystidicola cristivomeri* White, 1941 is considered a synonym of *C. stigmatura*. *Cystidicola stigmatura* is distinguished from the only other species in the genus, namely *C. farionis* Fischer, 1798, by the presence of lateral lobes on the eggs rather than filaments. A neotype of *F. stigmatura* is designated. *Cystidicola stigmatura* has not been found in fishes in the Great Lakes since 1925. The parasite was found in museum specimens of lake trout (*Salvelinus namaycush*) collected before 1925, suggesting that the species became rare or disappeared with the decline of lake trout in these lakes.

BLACK, G. A. 1983. Taxonomy of a swimbladder nematode, *Cystidicola stigmatura* (Leidy), and evidence of its decline in the Great Lakes. Can. J. Fish. Aquat. Sci. 40: 643 – 647.

Après examen des exemplaires de la collection de Leidy, *Cystidicola stigmatura* (Leidy, 1886) Ward et Magath, 1917 est considéré comme espèce valide. *Cystidicola cristivomeri* White, 1941 est considéré comme synonyme de *C. stigmatura*. Ce dernier se distingue de l'unique autre espèce du genre, *C. farionis* Fischer, 1798, par la présence de lobes latéraux plutôt que de filaments sur les oeufs. Nous désignons un néotype de *F. stigmatura*. *Cystidicola stigmatura* n'a pas été trouvé chez les poissons des Grands Lacs depuis 1925. On a rencontré le parasite dans des exemplaires de musée de touladi (*Salvelinus namaycush*)

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collectionné avant 1925, ce qui donne à croire que le nématode est devenu rare ou a disparu en même temps que déclinait le touladi dans ces lacs.

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TWO species in the genus *Cystidicola* are recognized; both are parasites of the swimbladder of salmonid fishes. *Cystidicola farionis* Fischer, 1798 is holarctic in distribution and most commonly infects whitefish (*Coregonus* spp.), trout (*Salmo* spp.), and Arctic char (*Salvelinus alpinus*) (Bykhovskaya-Pavlovskaya et al. 1962; Kennedy 1974; Margolis and Arthur 1979; G. A. Black unpublished data). The other species, presently called *C. cristivomeri* White, 1941, occurs only in North America and is a parasite of lake trout (*Salvelinus namaycush*) and Arctic char. The two species are distinguished by the morphology of their eggs. *Cystidicola farionis* has filamented eggs whereas *C. cristivomeri* has lateral lobes on the eggs.

Cystidicola stigmatura (Leidy, 1886) Ward and Magath, 1917 has been considered a synonym of *C. farionis* (Campana-Rouget 1955; Moravec and Ergens 1970; Arthur et al. 1976; Margolis and Arthur 1979). However, Leidy (1886) did not describe the morphology of the egg of this nematode. Later workers assumed that *C. stigmatura* had filamented eggs (Skinker 1931; Campana-Rouget 1955; Ko and Anderson 1969; Moravec and Ergens 1970; Arthur et al. 1976; Margolis and Arthur 1979) and thus considered *C. stigmatura* a synonym of *C. farionis*. However, evidence presented by Lankester and Smith (1980) cast doubt on this relationship. In the present study, Leidy's specimens were examined and it will be shown that *C. cristivomeri* is a synonym of *C. stigmatura*.

Materials and methods — The following specimens were examined from the United States National Museum (USNM): (a) *Filaria stigmatura* USNM 55 identified by Dr J. Leidy (no date given), (b) *Cystidicola stigmatura*, USNM 50664-50666 and 52058, collected from lake trout in Lake Michigan in 1894 and identified by Drs H. B. Ward and T. B. Magath (no date given). In addition, specimens of *Cystidicola stigmatura* from the Academy of Natural Sciences of Philadelphia ANSP 192 were examined. These specimens were initially identified by Dr J. Leidy as *Filaria stigmatura* and later determined to be *C. stigmatura* by Walton (1928). All nematodes were cleared and examined in glycerine.

Swimbladders of lake trout from the following museums were examined for nematodes: (a) Canadian National Museum of Natural Sciences, Ottawa, Ontario; (b) Royal Ontario Museum, Toronto, Ontario; (c) United States National Museum of Natural History, Washington, DC; (d) University of Michigan Museum of Zoology, Ann Arbor, Michigan; (e) Cornell University Langmuir Laboratory, Ithaca, New York. All fish had been preserved in toto. An incision along the visceral wall was either made or an existing one extended to allow access to the swimbladder. The organ was cut longitudinally and the lumen examined. Nematodes recovered were identified by examining eggs (100×) dissected from the uteri of female parasites (Ko and Anderson 1969; Lankester and Smith 1980).

Results and discussion — The label in the vial of Leidy's specimens (USNM 55) confirmed that these nematodes were collected by Dr J. H. Bissel from lake trout from Lake Superior (no date given) as were the worms used by Leidy (1886) in the original description of *F. stigmatura*. These specimens (USNM 55) and those of *C. stigmatura* identified by Drs H. B. Ward and T. B. Magath (USNM 50664-50666 and 52058) and by Walton (1928) (ANSP 192) agree with the description of *C. cristivomeri* given in White and Cable (1942) and Ko and Anderson (1969). Thus *C. stigmatura* is removed from the synonymy of *C. farionis* and *C. cristivomeri* is made a junior synonym of *C. stigmatura*.

Leidy (1886) did not designate either a holotype or type series of *F. stigmatura*. Consequently, one female specimen from Leidy's collection (USNM 55) has been designated as a neotype of *F. stigmatura* (USNM 77420). The major dimensions of the **neotype** are as follows:

Length 32.7 mm. Buccal length 233 μm. Nerve ring 377 μm from anterior end. Width at nerve ring 130 μm. Excretory pore 618 μm from anterior end. Muscular oesophagus 379 μm. Glandular oesophagus 1835 μm. Gonad 7.6 mm from anterior end. Vulva 15.3 mm from anterior end. Tail length 243 μm. Eggs (10 measured) 43−47 μm (45) by 18−19 μm (18) bearing a pair of lateral lobes.

This specimen agrees with descriptions of *F. stigmatura* in Leidy (1886) and of *C. cristivomeri* in White and Cable (1942) and Ko and Anderson (1969). The reader is referred to either of the latter two sources for a more complete description of this species. In addition, a description of the morphological development of the species is given in Smith and Lankester (1979) and Black and Lankester (1980). Furthermore, sizes obtained by the nematode in fishes in the wild are reported in Lankester and Smith (1980) and Black and Lankester (1981). Specimens of *C. stigmatura* from Greenwater Lake, Ontario (48°34′N × 90°26′W) have been deposited as voucher specimens (USNM 77317) to supplement Leidy's original material. Thus, the two known species of *Cystidicola* are:

1) *Cystidicola farionis* Fischer, 1798

SYNONYMS: *Cystidicola canadensis* Skinker, 1930
Cystidicola stigmatura of Skinker 1931 *not* (Leidy, 1886)
Cystidicola stigmatura of Ko and Anderson 1969 *not* (Leidy, 1886)

TYPE LOCALITY: Europe

NORTH AMERICAN HOSTS: *Coregonus artedii*, *C. clupeaformis*, *C. hoyi*, *C. reighardi*, *Oncorhynchus gorbuscha*, *O. kisutch*, *O. nerka*, *O. tshawytscha*, *Osmerus mordax*, *Prosopium cylindraceum*, *P. williamsoni*, *Salmo gairdneri*, *Salvelinus alpinus*, *S. fontinalis*, *S. fontinalis* × *S. namaycush*, *S. namaycush*, *Thymallus arcticus*

FIG. 1. Areas in the Great Lakes from which lake trout were examined for *Cystidicola stigmatura* (= *C. cristivomeri*). Location of Ward and Magath's specimens from northern Lake Michigan is included on the map. All positive records of *C. stigmatura* are from lake trout collected prior to 1925.

2) *Cystidicola stigmatura* (Leidy, 1886) Ward and Magath, 1917

SYNONYMS: *Cystidicola cristivomeri* White, 1941
Cystidicola farionis of Ward and Magath 1917 *not* Fischer, 1798
Cystidicola sp. of White 1940
Ancyracanthus cystidicola of Wright 1879 *not* Lamarck, 1801
Filaria stigmatura Leidy, 1886

TYPE LOCALITY: Lake Superior

NORTH AMERICAN HOSTS: *Salvelinus alpinus*, *S. fontinalis*, *S. namaycush*

COMMENTS: Wright (1879) reported *A. cystidicola* from lake trout from Lake Superior. Since *C. farionis* does not mature in this host in this lake (Lankester and Smith 1980; this study, see below) this report is referred to *C. stigmatura*. Similarly, the report of *C. farionis* in lake trout in Lake Erie (Ward and Magath 1917) probably pertained to *C. stigmatura*.

The taxonomic confusion surrounding the species of *Cystidicola* began when Leidy (1886) proposed *C. stigmatura* but did not describe the lateral lobes on the eggs to distinguish it from *C. farionis*. Ward and Magath (1917) apparently did not recognize the morphological distinction between these species, particularly with reference to the eggs. For example, nematodes which they identified as *C. stigmatura* and deposited in the USNM have lateral lobes on the eggs; in contrast, Dr H. B. Ward provided Skinker (1931) with specimens he identified as *C. stigmatura* from *Coregonus* spp. which had filamented eggs. Thus both lake trout and *Coregonus* spp. were regarded as suitable hosts of *C. stigmatura*. Skinker (1931) redescribed *C. stigmatura* from specimens collected from *Coregonus* spp.; hence, later workers (Campana-Rouget 1955; Ko and Anderson 1969; Moravec and Ergens 1970; Arthur et al. 1976; Margolis and Arthur 1979) considered this species to have filamented eggs.

Cystidicola stigmatura is apparently absent in the Great Lakes and has not been found in recently collected lake trout (Table 1)[1]. The parasite was found in museum specimens of lake trout from Lakes Superior, Huron, and Michigan although only in fish collected prior to 1925 (Fig. 1; Table 1). The nematode probably occurred in Lakes Erie and Ontario as

TABLE 1. Prevalence of *Cystidicola stigmatura* (= *C. cristivomeri*) in lake trout collected from the Great Lakes.

Lake	1883–1925	1926–77[a]
Superior	3/11[b]	0/89[c]
Huron	1/2	0/27[d]
Michigan	2/8	—
Erie	—	0/5
Ontario	0/7	0/3

[a]All lake trout from Lakes Superior and Huron were collected after 1935.
[b]Number of lake trout infected/number examined.
[c]Includes 44 lake trout in Lankester and Smith (1980).
[d]Includes 15 lake trout in Bangham (1955) and 4 lake trout in Lankester and Smith (1980).

[1]Neither were mature *C. farionis* found.

well. Its presence in Lake Erie has already been discussed. *Cystidicola stigmatura* has not been reported in Lake Ontario although it occurs in the drainage basin in Big Ohlmann Lake, Ontario (45°03′N 77°00′W) (unpublished data). The parasite probably dispersed to Big Ohlmann Lake via glacial Lake Iroquois (unpublished data). Since this glacial lake covered present day Lake Ontario (Prest 1970) the parasite was probably present in the lake at one time (see below).

The absence of *Cystidicola stigmatura* from lake trout collected from large areas of the Great Lakes over the last 50 yr (Fig. 1; Table 1) suggests that *C. stigmatura* may have disappeared with the decline of lake trout populations during the last century, as was suggested by Lankester and Smith (1980). Lake trout were scarce in Lake Ontario at the turn of the century, increased in the 1920s and disappeared during the 1940s and 1950s (Christie 1963, 1973). Lake trout were considered extinct in Lake Erie by the mid-1930s (Hartman 1973). Populations in the upper three lakes (Superior, Huron, and Michigan) gradually declined through the early 1900s and then crashed after the invasion of the sea lamprey (*Petromyzon marinus*) in the 1940s and 1950s (Berst and Spangler 1972; Pycha and King 1975; Brown et al. 1981). The decline in numbers of lake trout probably caused the extinction of the parasite in some of the lakes. However, some local populations of native lake trout still exist (Dehring et al. 1981) and *C. stigmatura* may have survived in these remnant populations.

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Precocious Male Atlantic Salmon Parr (*Salmo salar*) in Insular Newfoundland

E. L. DALLEY,[1] C. W. ANDREWS,[2] AND J. M. GREEN[3]

Department of Biology, Memorial University of Newfoundland, St. John's, Nfld. A1B 3X9

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The incidence of sexual precocity in male Atlantic salmon parr (*Salmo salar*) was examined in selected rivers in insular Newfoundland from 1974 to 1977. The incidence was variable but generally high, particularly in eastern rivers. Examination of age-specific lengths revealed that the faster growing males became precocious but percent precocity for these varied among river systems. Precocity did not influence growth of parr in comparison to immatures up to the smolt stage. No difference was found in the condition (using gutted weights) of mature and immature parr. However, condition deteriorated in precocious fish compared to immature fish with smoltification. Parr sex ratios frequently differed significantly from 1:1. Possible reasons are discussed in terms of sex related distribution patterns and mortality of precocious parr. From smolt runs examined, it appears that too few precocious parr migrate as smolt to contribute to the grilse population. As a result of the high mortality, rivers with a high percentage of sexually precocious males tend to have a corresponding high percentage of adult females.

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De 1974 à 1977, nous avons étudié l'occurrence de la précocité parmi les tacons de saumon (*Salmo salar*) mâles de rivières choisies de Terre-Neuve. Leur présence est variable mais généralement élevée, en particulier dans les rivières de l'est de la province. L'examen des longueurs à un âge donné indique que les mâles à croissance rapide ont une maturité sexuelle hâtive, mais que leur pourcentage varie d'un réseau fluvial à l'autre. La précocité n'influence pas la croissance des tacons jusqu'au stade de smolt, comparativement aux poissons immatures. Nous n'avons observé aucune différence de condition (fondée sur les poids éviscérés) chez des tacons matures et immatures. Cependant, la condition des poissons précoces se détériore avec la smoltification, comparativement aux poissons immatures. La proportion des sexes des tacons s'écarte souvent et de façon appréciable de 1:1. Nous en analysons les raisons possibles en fonction d'une distribution et d'une mortalité liées au sexe des tacons précoces. À en juger par les smolts examinés, il semble que les tacons précoces qui migrent comme smolts ne soient pas assez nombreux pour contribuer à la

[1]Present address: Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld. A1C 5X1.
[2]Deceased.
[3]Marine Sciences Research Laboratory.

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population de castillons. À cause de la forte mortalité, les rivières à fort pourcentage de mâles précoces ont tendance à avoir un pourcentage élevé correspondant de femelles adultes.

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ALTHOUGH the incidence of precocious males varies among stocks of Atlantic salmon, *Salmo salar* (Schaffer and Elson 1975), precocious sexual development is common over the geographic range of the species (Jones and Orton 1940; Sutterlin et al. 1978; Lee and Power 1976). It occurs in both natural and hatchery stocks. Mature parr are capable of fertilizing adult salmon eggs (Jones and King 1950) and Jones and King (1952) concluded that they can fertilize a considerable fraction of the eggs that are spawned.

The distribution and incidence of sexual precocity in Newfoundland Atlantic salmon has not been investigated despite the importance of such information in understanding the population dynamics of this species. Our study was therefore undertaken to determine the level of precocity in different areas of insular Newfoundland. Age and size of mature parr, sex ratios of parr and smolt, and growth and length–weight relationships of precocious and immature parr and smolt were also investigated. We also considered the relationship between precocious sexual development and characteristics of the adult salmon run.

Materials and methods — Samples of parr and smolt from Newfoundland river systems (Fig. 1) were collected using several methods. All samples of parr from rivers were electrofished. Those from ponds were caught in fyke traps (lake trap nets) except for part of the September 1974 sample from Fitzgerald's Pond which was caught in a 3-panel gillnet (square mesh sizes 12.7, 19.1, and 38.1 mm). Smolts were collected in fyke traps set across streams in such a way that all migrants were captured.

Samples, except smolt from Northeast and Southeast rivers in 1977 (which were examined fresh), were frozen within several hours. Later fork lengths to the nearest millimetre and gutted weights (visera and gonads removed) to the nearest 0.1 g were recorded. Sex was determined by examination of the gonads. Precocious males could be distinguished from immature males in early July by a definite anterior widening of the gonads as described by Jones (1940). Fish were placed into one of three categories: (1) precocious male; (2) immature male, or (3) immature female. At the time of processing scales were removed from the left side of specimens. Age was later determined according to the annulus method validated by Havey (1959).

The total smolt run of Northeast River was intercepted in 1977 using fyke traps. Since the proportions of spent males in the run was extremely low random sampling did not suffice to obtain a sample large enough for further analysis. Precocious males were therefore selectively chosen. It was discovered that spent male smolt could readily be distinguished from typical smolt in that they are not as silvery. Their lateral and ventral surfaces are a greyish brown with a copper tinge which is also prominent on the opercular cover and maxillary bone. Although parr marks are not visible, some red spots typical of parr are noticeable but mottled.

We used chi-square tests to investigate deviations from a 1:1 sex ratio. Where sufficient numbers were available a *t*-test or One Way Anova compared the lengths of the different age-classes of the groups and a Student-Newman-Keuls multiple range test (Steel and Torrie 1960) isolated any differences. Analysis of covariance was used to test for difference in length–weight relationships of the sex categories in each river system using log 10 (length) as the independent variable, x, and log 10 (weight) as the dependent variable, y. Weights used in the covariance analysis were those of eviscerated fish. This eliminated biases caused by food contents in the gut and of increased gonad weights in mature males. A *t*-test isolated any differences in intercepts and a Student-Newman-Keuls multiple range test any differences in slopes.

Results — Precocious male parr were found in all areas

TABLE 1. Percent precocity in samples of Atlantic salmon parr from insular Newfoundland. Shown are the percent of male parr that are sexually precocious in each age-group and in combined age-groups for each sample. (Numbers in brackets indicate number of male parr in sample.)

Sample	1+	2+	3+	4+	Combined age-groups
Salmonier River	100 (8)	100 (14)	100 (1)	100 (1)	100 (24)
Fitzgerald's Pond, Northeast River	93.8 (48)	87.5 (16)	100 (4)	—	92.6 (68)
Come by Chance River	85.7 (42)	85.7 (7)	100 (4)	—	86.8 (53)
North Harbour River (P.B.)	53.1 (32)	85.7 (7)	100 (4)	100 (1)	63.6 (44)
Bay de L'eau River	69.2 (26)	90.9 (11)	100 (3)	—	78.9 (40)
Rushoon River	100 (26)	100 (21)	100 (4)	100 (1)	100 (52)
Salmon Brook, Gander River	24.0 (25)	95.7 (46)	100 (9)	100 (1)	74.1 (81)
Tote Brook, Great Rattling Brook	0.0 (1)	40.0 (25)	72.0 (25)	100 (3)	57.0 (54)
Rocky Brook, Humber River	16.0 (25)	9.4 (32)	—	—	12.3 (57)
Lomond River	54.8 (42)	75.0 (4)	—	—	56.5 (46)
Western Arm Brook	—	62.5 (16)	88.9 (18)	100 (2)	77.8 (36)
$\bar{x}$ of all samples	59.7 (275)	75.7 (199)	95.7 (72)	100 (9)	72.7 (555)

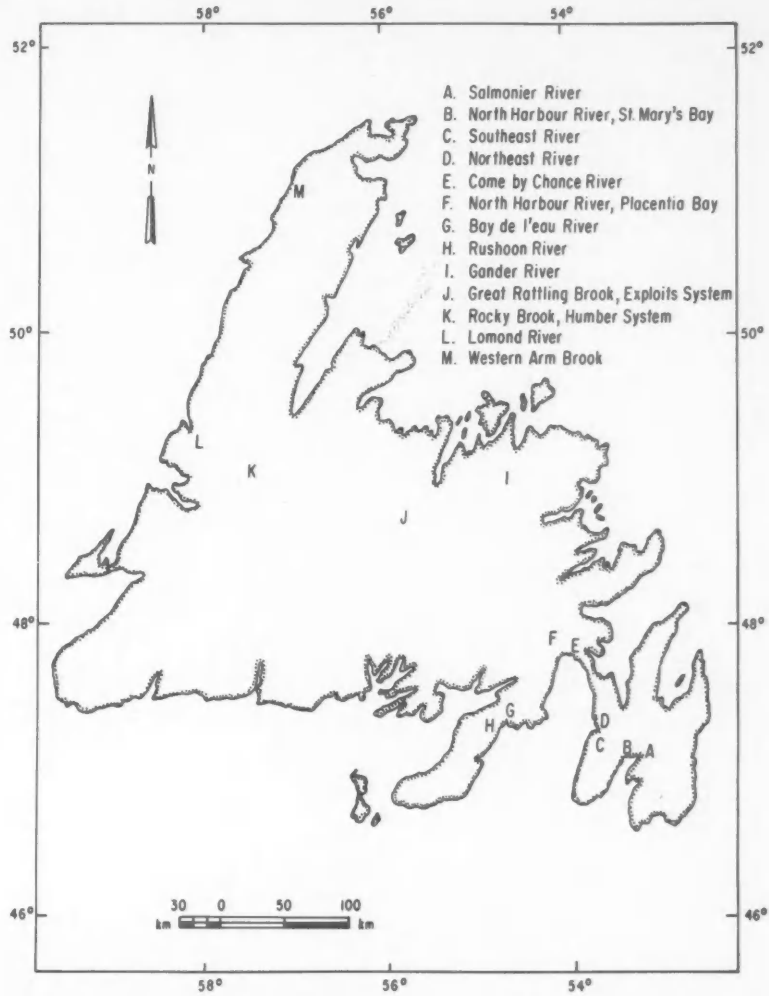

FIG. 1. Insular Newfoundland showing locations of river systems where samples of Atlantic salmon (*Salmo salar*) parr and smolt were taken.

sampled. The percent occurrence was variable depending on age and location (Table 1), and overall ranged from 12.3% of male parr in Rocky Brook to 100% in Salmonier and Rushoon rivers; mean overall incidence being 72.7%. Less than 2% of all precocious parr collected were older than 3+, but all parr older than 3+ were precocious (Table 1). All parr older than 2+ in samples from rivers entering Placentia and St. Mary's bays were precocious. Sex ratios of parr often deviated significantly from 1:1 (Table 2), and in all except one (Fitzgerald's Pond, October 1976) in favor of males.

Mean lengths of males that matured at 1+ ranged from 72.6 to 116.1 mm, and the smallest precocious parr taken in any of the samples was 60 mm. Mean lengths of precocious 1+ males were greater than those of immature males in all samples (significantly ($P < 0.001$) in one) but this relationship did not hold for older age-groups. There were no such trends and no significant differences in any comparisons of lengths of 2+ and older parr.

Analysis of covariance indicated a significant difference in the length–weight relationships of mature and immature fish in two samples. Precocious male parr from Salmon Brook, Gander River had a significantly higher intercept ($P < 0.01$) than immature female parr indicating that the condition of the precocious males was better than that of the females. The

TABLE 2. Sex ratios of Atlantic salmon parr from Newfoundland rivers and the results of testing for significant differences for each age-group within the sample and for the overall sample by chi-square tests.

Age	Male	Female	*P*
Fitzgerald's Pond, September 1974			
1+	48	51	None
2+	16	68	<0.001
3+	4	14	<0.02
Total	68	133	<0.01
Junction Pond, June 1977			
1+	20	20	None
2+	35	22	None
3+	31	3	<0.001
4+	3	0	None
Total	89	45	0.001
Come by Chance, October 1975			
1+	42	28	None
2+	7	0	<0.01
3+	4	1	None
Total	53	29	<0.01
Bay de L'eau River, Sept.–Oct. 1975			
1+	26	29	None
2+	11	5	None
3+	3	0	None
Total	40	34	None
Salmonier River, July 1976			
1+	8	1	<0.02
2+	14	8	None
3+	1	0	None
4+	1	0	None
Total	24	9	<0.01
Tote Brook, August 1976			
1+	1	5	None
2+	25	24	None
3+	25	20	None
4+	3	3	None
Total	54	52	None
Lomond River, August 1976			
1+	42	37	None
2+	4	1	None
Total	46	38	None
Fitzgerald's Pond, July 1975			
1+	36	35	None
2+	2	2	None
3+	2	—	None
Total	40	37	None
Churchills Pond, Come by Chance River, July 1975			
1+	42	24	<0.05
2+	7	3	None
3+	5	0	<0.05
Total	54	27	<0.05
North Harbour River, October 1975			
1+	32	17	<0.05
2+	7	5	None
3+	4	0	<0.05
4+	1	0	None
Total	44	22	<0.01
Rushoon River, September 1975			
1+	26	18	None
2+	21	33	None
3+	4	2	None
4+	1	0	None
Total	52	53	None
Salmon Brook, August 1976			
1+	25	12	<0.05
2+	46	18	<0.001
3+	9	2	<0.05
4+	1	—	None
Total	81	32	<0.001
Rocky Brook, August 1976			
1+	25	20	None
2+	32	39	None
3+	0	3	None
Total	57	62	None
Western Arm Brook, August 1977			
2+	16	8	None
3+	18	10	None
4+	2	0	None
Total	36	18	<0.02

smolt samples from Northeast River had significantly different slopes. The slope of the length–weight relationship of immature female smolt was significantly greater ($P < 0.05$) than that of precocious male smolt. As smolt increase in length the gutted-weight at length of precocious males decreases relative to the gutted-weight at length of immature females.

The sex ratio of 111 parr collected from the spawning ground in Northeast River in 1975 was 98.2% in favor of precocious males and 100% of 76 collected in 1976. Examinations of the ages of these revealed that over 95% of the precocious males on the spawning ground in Northeast River were 1–3 yr old while the oldest were 5+ yr.

The sex ratios of four samples of smolts from rivers entering St. Mary's Bay (North Harbour River) and Placentia Bay (Northeast River, 1975, 1976; Southeast River) were highly in favor of females (range of 81–91.8%). Immature males constituted only 4–10.3% of the runs. The age compositions of typical and spent male smolt from Northeast River were quite similar with approximately 85% of both groups being 3+. Only 6% of typical smolt and 9.5% of precocious spent smolt were older than 3+.

Discussion — Sex ratios — Although deviations from a 1:1 sex ratio have been reported in various life history stages of Atlantic salmon, it is generally believed that there is a 1:1 ratio at hatching (Österdahl 1969). In all except one of our parr samples (September, Fitzgerald's Pond) that had a sex ratio significantly different from 1:1 the sex ratio was in favor of males (Table 2). Belding (1937) reported that males outnumbered females in the older age-classes of parr in some west Newfoundland rivers. Power (1973) explained this phenomenon as a result of males not smoltifying. This is exemplified by our sample from Junction Pond in June. The sample, highly in favor of males, ($P < 0.001$) was taken just following the smolt run which had a sex ratio 90% in favor of females. There are, however, sex ratios in favor of males that cannot be explained by this mechanism since it is prior to the age of smoltification. This can be accounted for by the migration of precocious male parr to spawning areas prior to the spawning season as suggested by King (1947). The sex ratio in favor of females in a nonspawning area (Fitzgerald's Pond) in September attests to this as do the two samples from the spawning grounds that were composed almost entirely of mature males. This suggests that samples which intercept or neglect a significant number of these migrating parr will give an inaccurate indication of the primary sex ratio.

Growth and length–weight relationships — Alm (1959) and Bailey et al. (1980) reported that the larger parr within an age-group tend to mature earlier. In all cases where the length of 1+ immature and precocious males could be compared the precocious male parr were larger than immature males, and in Come by Chance River this difference was significant ($P < 0.001$).

While within a particular population the faster growing parr may be most likely to exhibit precocial sexual development, it is evident from our data that other factors are necessary for maturation. Both Fitzgerald's Pond and Rushoon River parr had relatively high growth rates and a high percent precocity, while Rocky Brook, which also had a relatively high growth rate, had a low percent precocity. Come by Chance River parr, which had slower growth than adjacent North Harbour River parr at 1+, had a precocity of 85.7% while North Harbour River had only 53.1%. Salmon Brook parr had faster growth than Come by Chance parr but had only 24% mature at 1+. On the other hand, Tote Brook parr, which had the

slowest growth rate of all samples, had a precocity of only 40% at 2+, the lowest incidence of any 2+ sample except Rocky Brook. Thus while growth rate may affect the incidence of precocity, fast growth alone does not necessarily result in a high percent precocity.

Growth of the faster growing precocious parr is slowed by maturation since after the first year precocious males are not consistently longer than immature males. In Fitzgerald's Pond, Come by Chance River, North Harbour River, Salmon Brook and Lomond River 2+ immature parr were as long or longer than the precocious males. In immature fish surplus energy is equivalent to total somatic growth, whereas after sexual maturity it is subdivided into energy added as body substance and the amount liberated as sexual products (Ware 1980). Length–weight relationships of nonmaturing and maturing parr were compared to investigate any effect on somatic tissues of the reduction in energy available to growth during gonadal maturation. The condition of precocious parr was not significantly lower than immature parr, and, in fact, in one sample (Gander River) it was better than that of eviscerated immature female parr. Although maturation may reduce fat deposits in the body cavity as described by Leyzerovich (1973), it apparently does not affect the condition of parr to the extent that somatic tissues of the body are reduced compared with immature fish.

In smolt, however, the condition of precocious males was reduced compared to that of immature females. As length increased the difference in the weights of precocious male (spent) smolt and immature female smolt became greater. Smoltification results in a sharp fall in energy reserves (Hoar 1976) and it appears that although the energy cost of maturation is low enough to be undetectable by examination of length–weight regressions of eviscerated mature and immature parr, the added energy requirements of smoltification results in detectable differences in the length–weight relationships of immature and mature smolt.

Gebhards (1960) and Mitans (1973) have documented an increased mortality of precocious salmonid parr following spawning, and Leyzerovich and Mel'nikova (1979) have suggested that these fish have higher mortality than their cohorts during and following smoltification. Our data indicate that upon reaching the stage of smoltification only a small percentage of precocious male Atlantic salmon parr in insular Newfoundland actually smoltify and there is high mortality in the remaining fish. This is elucidated by (1) the deterioration in condition of those precocious (spent) males that appear in the smolt run compared to that of immature smolt, (2) sex ratios of smolt highly in favor of females and (3) the low percentage of precocious males residing in freshwater that are older than the age of smoltification.

Adult salmon run — Two characteristics of adult salmon returning to the majority of Newfoundland rivers are: (1) an extremely high proportion (sometimes up to 100%) of grilse (Moores et al. 1978), and (2) a sex ratio in most areas highly in favor of females (Chadwick et al. 1978; Davis and Farwell 1975). Although evidence presented here does not explain the high proportion of grilse, it does illustrate that mechanisms thought to occur elsewhere do not operate in insular Newfoundland. On the North Shore of the Gulf of St. Lawrence an increase in the incidence of precocious males results in an increase in the number of males that return as grilse (Schiefer 1971). This mechanism does not operate here where too few precocious males smoltify to contribute significantly to the numbers of returning grilse. Where the incidence of precocity is low (eg. 12.3% in Rocky Brook of the Humber System) the adult sex ratio will not be as highly in favor of females (eg. the Humber System (Davis and Farwell 1975)) and where precocious male parr survive spawning and smoltification a high proportion of adult males might be grilse as on the North Shore of the Gulf of St. Lawrence. Where the incidence of precocity is high and there is a high mortality of precocious parr and smolt as in insular Newfoundland the sex ratio of grilse highly in favor of females is accounted for.

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Measurements of Benthic Macroinvertebrate Standing Crop from the Canadian Continental Shelf and Slope of Southern Davis Strait and Ungava Bay

PATRICK L. STEWART[1]

MacLaren Plansearch Limited, Suite 1020 Cogswell Tower, 2000 Barrington Street, Halifax, N.S. B3J 3K1

STEWART, P. L. 1983. Measurements of benthic macroinvertebrate standing crop from the Canadian continental shelf and slope of southern Davis Strait and Ungava Bay. Can. J. Fish. Aquat. Sci. 40: 652–658.

Benthic macroinvertebrate standing crop at 14 stations on the Canadian continental shelf, southeast of Baffin Island, ranged from 19.8 to 479.9 g/m^2 and was about the same size for given depths, as reported for the Grand Banks of Newfoundland, and higher than reported in more southerly portions of the eastern North American continental shelf. Standing crop was correlated negatively with depth and sediment content of both fine and medium sand.

STEWART, P. L. 1983. Measurements of benthic macroinvertebrate standing crop from the Canadian continental shelf and slope of southern Davis Strait and Ungava Bay. Can. J. Fish. Aquat. Sci. 40: 652–658.

La biomasse de macro-invertébrés benthiques à 14 stations sur le plateau continental canadien, au sud-est de l'île Baffin, varie de 19,8 g/m^2 à 479,9 g/m^2 et a à peu près la même importance, à des profondeurs données, que celle qu'on a rapportée pour les Grands bancs de Terre-Neuve. Mais elle dépasse la biomasse des portions plus méridionales du plateau continental de l'est de l'Amérique du Nord. On a trouvé une corrélation négative entre la biomasse et la profondeur, et le contenu en sédiment, à la fois du sable fin et du sable de moyenne grosseur.

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SEVERAL recent studies of benthic invertebrate communities on the continental shelf and slope of eastern North America contributed information on standing crop. The southern Labrador Shelf, Newfoundland Grand Banks, St. Pierre and Banquereau Banks, and Scotian Shelf on the Canadian eastern seaboard were examined by Nesis (1965). Mills and Fournier (1979) and Mills (1980) studied the Halifax section of the Scotian Shelf and Mills (1975) studied Nain Bay, Labrador. Studies on the middle eastern Atlantic seaboard of North America include the Gulf of Maine (Rowe et al. 1975), Georges Bank (Wigley 1961), the New England continental slope and rise (Haedrich and Rowe 1977) and shelf depths (Rowe et al. 1974; Wigley et al. 1976), and the Gulf of Mexico (Rowe et al. 1974). The northern continental shelves

[1]Present address: Box 109, Newport, N.S. B0N 2A0.

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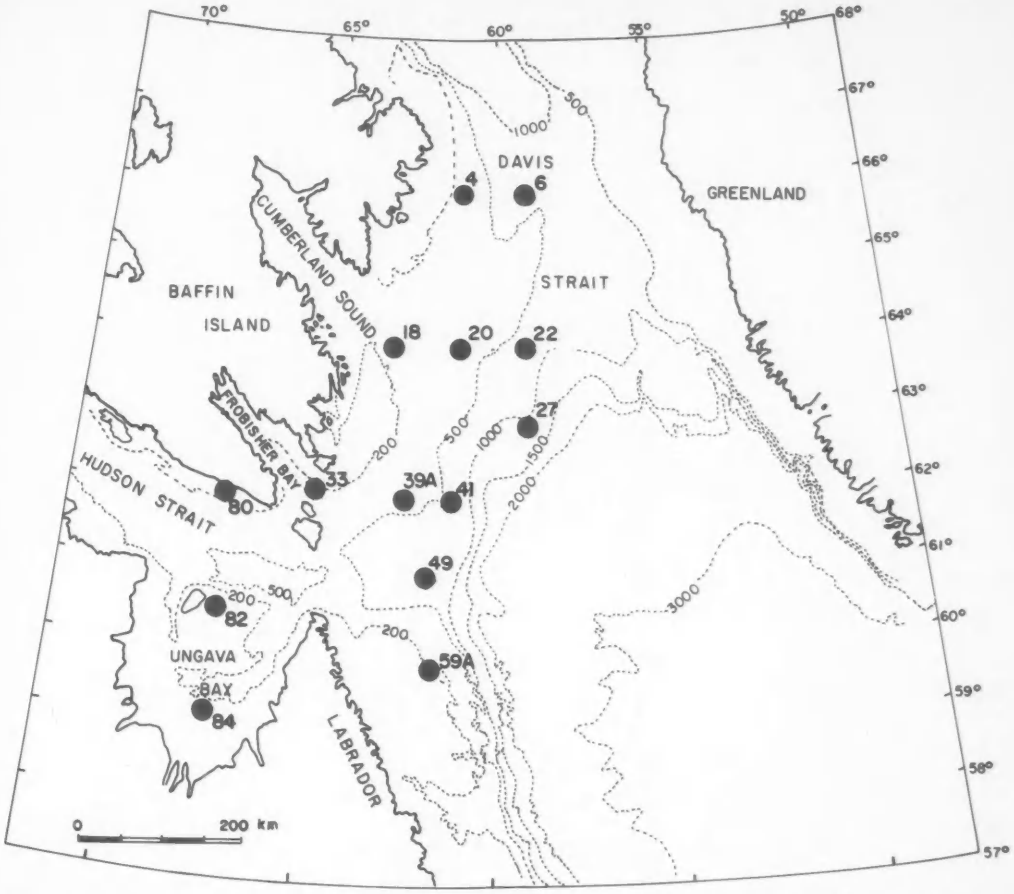

FIG. 1. Station locations for benthic invertebrate sampling in southern Davis Strait and adjacent areas in 1977 and 1978. Depth contours are in metres.

of North America, including the Labrador Shelf north of 52°N, the Baffin Island continental shelf, and the shelf in Ungava Bay, have been largely neglected in quantitative benthic studies, with the exception of a study by Ellis (1960) on the nearshore subtidal marine benthic invertebrates of northeastern Baffin Island and West Greenland.

Many of these studies examined the relationship of standing crop with water depth, but few sought to assess the relationship between standing crop and other physical factors such as bottom sediment type or temperature. Substrate type, temperature, and latitude are known to affect benthic community structure and animal physiological processes, but their influence on standing crop is unknown.

This study was conducted to collect information on standing crop and community composition of benthic macroinvertebrates on the continental shelf and slope of Baffin Island, in Ungava Bay, and on the northern Labrador Shelf in support of petroleum exploration activities in the southern Davis Strait. The survey represents the first quantitative benthic sampling of the continental shelf in the area. Information on benthic invertebrate standing crop from the survey and an analysis of factors affecting it are presented.

Study area — Benthic sampling was conducted in August–September 1977 and April 1978 on three cruises of the MV *Lady Johnson II* in the waters off southeastern Baffin Island. Fourteen stations were chosen to give broad geographic coverage of the southeastern Baffin Island shelf and slope and adjacent waters (Fig. 1).

Nearly all of the study area lies on the deep Baffin Island continental shelf. Depth increases gradually offshore from Baffin Island to the shelf edge at a depth of about 600 m (Fig. 1). Stations 22 and 27 at 920 and 970 m, respectively, lie just beyond the shelf edge. Shallow trenches ending

TABLE 1. Standing crop (g/m^2 wet wt) and numerically dominant species of benthic invertebrates in the present study.

Station	Standing crop (g/m^2)	Standard deviation	Range	No. of samples	Numerically dominant species
4	21.1	25.1	1–52	4	*Lumbrinereis impatiens*, *Ophiura robusta*
6	45.9	44.1	15–132	7	*Terebellides stroemi*
18	29.4	19.2	8–57	7	*Myriochele oculata*, *Prionospio cirrifera*
20	28.1	15.7	12–63	8	*Onuphis conchylega*, *Prionospio cirrifera*
22	69.6	34.0	31–108	5	*Astarte crenata*, *Haploops tubicola*
27	50.2	38.2	18–118	6	*Lumbrinereis fragilis*, *Aricidea suecica*
33	159.4	39.6	131–187	2	*Ophiura robusta*, *Ischyrocerus latipes*
39A	55.4	48.9	2–146	7	*Glycera capitata*, *Ophiura robusta*
41	38.9	10.0	23–48	6	*Glycera capitata*, *Syllis cornuta*
49	19.8	13.2	7–47	7	*Ischyrocerus megacheir*, *Haploops tubicola*
59A	112.6	98.1	32–267	7	*Rhodine gracilior*, *Maldane sarsi*
80	109.3	48.1	67–189	5	*Onuphis conchylega*, *Ophiura robusta*
82	479.9	340.4	185–1193	7	*Ophiura robusta*, *Ampelisca eschrichti*
84	388.7	171.8	142–581	7	*Aglaophamus malmgreni*, *Eudorellopsis integra*

TABLE 2. Physical characteristics of Davis Strait stations.

Station	Bottom temperature (°C)	Sediment composition (%)						Median grain size (μm)	Inman sorting index	Depth (m)
		Gravel	Coarse sand	Medium sand	Fine sand	Silt	Clay			
4	1.4	0.0	0.4	0.4	34.7	49.0	15.6	41	2.2	622
6	1.4	0.0	3.1	3.9	13.4	56.9	22.6	16	2.9	658
18	−0.2	0.1	3.7	10.0	69.6	14.8	1.9	108	0.7	292
20	2.2	2.5	2.1	5.3	68.5	18.5	3.1	67	0.6	283
22	2.9	—	—	—	—	—	—	—	—	920
27	3.0	0.3	5.8	3.4	24.8	48.3	17.3	29	3.1	970
33	0.4	—	—	—	—	—	—	—	—	177
39A	4.3	1.7	10.8	9.6	47.6	25.1	5.1	88	1.7	507
41	4.3	40.4	7.2	7.7	21.9	19.0	3.6	376	4.6	532
49	4.0	0.5	2.2	1.1	29.8	59.0	7.3	44	1.2	621
59A	3.0	2.0	12.1	23.1	46.9	11.6	4.4	177	1.6	180
80	0.7	27.6	9.6	14.7	44.6	1.7	1.8	268	2.7	179
82	0.0	43.5	10.4	5.2	13.9	18.9	8.1	616	4.2	106
84	−0.7	0.5	1.7	1.2	14.0	65.7	16.7	31	2.6	145

in Cumberland Sound partition the bottom adjacent to Baffin Island into several banks (depths of 100–200 m). The shallowest occurs around Lady Franklin Island (62°55′N, 63°43′W), but one also occurs along the northern coast of Frobisher Bay (station 33). Ungava Bay is a shallow shelf with a deep channel underlying Hudson Strait. On the northern side of Hudson Strait, depth decreases gradually toward Baffin Island.

Methods — Van Veen grab samples (0.1 m^2) were taken at each station. The volume of each sample was measured, and only those having volumes near the maximum for each station were analyzed. Samples were cleaned by suspending them in running seawater and then passing the suspension through a 0.42-mm sieve. Animals retained by the sieve or not suspended by the procedure were stored in 10% unbuffered formalin. They were later rinsed with freshwater over a 0.5-mm

TABLE 3. Pearson product moment correlations (r) between physical and biological variables at benthic stations.

	Log_{10} standing crop	Bottom temperature	Gravel	Coarse sand	Medium sand	Fine sand	Silt	Clay	Median grain size	Inman sorting index	Depth	Log_{10} depth
Standing crop	0.93	−0.59	0.44	0.24	−0.09	−0.49	0.05	0.14	0.56	0.44	−0.56	−0.73
Log_{10} standing crop		−0.51	0.43	0.46	0.18	−0.44	−0.10	0.09	0.53	0.46	−0.53	−0.71
Bottom temperature			−0.05	0.24	0.13	0.05	−0.03	−0.20	−0.13	−0.02	0.54	0.62
Gravel				0.49	0.14	−0.32	−0.50	−0.36	0.94	0.74	−0.34	−0.40
Coarse sand					0.76	0.03	−0.67	−0.46	0.60	0.30	−0.32	−0.37
Medium sand						0.44	−0.76	−0.59	0.26	−0.14	−0.45	−0.39
Fine sand							−0.58	−0.68	−0.23	−0.78	−0.24	−0.08
Silt								0.83	−0.57	−0.03	0.51	0.44
Clay									−0.41	0.28	0.50	0.37
Median grain size										0.63	−0.47	−0.55
Inman sorting index											0.10	−0.04
Depth												0.96
Log_{10} depth												

screen, sorted into major taxa, blotted dry, and weighed to the nearest 0.01 g to estimate formalin-preserved wet weight (Rowe and Menzel 1971). Weighing took place within 2 mo of sampling and no deterioration of mollusc shells was noted as a result of storage of samples in unbuffered formalin.

Sediment samples were taken for grain size analysis at all stations except 22 and 33, the former a silty clay bottom and the latter a coarse sand bottom with some rocks and gravel. Grain size distribution in Wentworth size grades was determined by pipette analysis and dry sieving (Krumbein and Pettijohn 1938). Median grain size (millimetres) and Inman sorting index were calculated from cumulative frequency distributions. The Inman index (calculated as $\frac{1}{2}(\phi\ 84\% - \phi\ 16\%)$ is largest when the percent occurrence of all size classes is uniform and thus the sediment is most heterogeneous.

Bottom water temperature was measured by bathythermograph at depths shallower than 200 m and taken from the results of physical oceanographic measurements made in the area during the baseline environmental program (Seaconsult Marine Research Limited 1978) and from a Fisheries and Oceans Canada survey of pink shrimp in the area in August 1978.

I calculated simple Pearson product moment correlations between standing crop and physical variables determined at each station. The $\log_{10}$ transformation was applied to depth, and an arcsine transformation was applied to the proportion of various sediment grades. I examined possible significant relationships further by determination of partial correlations among specific variables when some of the more significant factors were controlled (their linear effects removed). Correlation and partial correlation analyses were conducted by computer using SPSS (Statistical Package for the Social Sciences) (Nie et al. 1970).

Results — Benthic invertebrate standing crop is presented in Table 1, and sediment physical characteristics, bottom water temperature, and depths of benthic stations are presented in Table 2. Standing crop was highly variable, with the standard deviation of measurements greater than 50% of the mean at 9 of 14 stations (Table 1). It was highest at stations 82 and 84 in Ungava Bay (479.9 and 388.7 g/m^2, respectively) and lowest ($\leq 30\ g/m^2$) at stations 4, 18, 20, and 49 (Table 1). Several pairs of stations, which occurred at similar depths in the same geographical area (18 and 20, 39A and 41, and 22 and 27), also had similar macroinvertebrate standing crop.

Standing crop at stations 82 and 84 was completely dominated by single species: the brittlestar, *Ophiura robusta* Ayres, at station 82 and the bivalve mollusc, *Macoma calcarea* Gmelin, at station 84. These species contributed approximately 43 and 70% of total standing crop at these stations, respectively. At station 4, large quantities of sponge spicules (1040 g/m^2, range 471−1952 g/m^2) were present, complementing standing crop of other invertebrates.

The most significant simple correlation of standing crop with other physical variables was with $\log_{10}$ depth ($r = -0.73$, Table 3). However, standing crop was also significantly negatively correlated with bottom temperature and fine sand content and was positively correlated with sediment median grain size, content of gravel, and sorting index

TABLE 4. Formalin-preserved wet weight standing crops (g/m^2) of benthic invertebrates measured for different depth intervals by researchers working on the eastern continental shelf and slope of North America (number of samples used to calculate standing crop in parentheses).

Reference	Depth interval (m)					
	0–50	50–100	100–200	200–300	300–500	500–1000
Nesis 1965	1455(6)	312(23)	76(35)	53(31)	48(40)	46(16)
Rowe et al. 1974	5.1(2)	4.4(2)	3.7(1)	—	—	12.0(1)
Rowe et al. 1975	—	—	—	27.6	—	—
Mills 1975	458(7)	—	—	—	—	—
Mills 1980	—	20.4	—	—	14.1	—
Ellis 1960						
Mud	200(20)	—	—	—	—	—
Sand–mud	438(23)	—	—	—	—	—
Wigley et al. 1976	266	189	79	—	28[1]	12
This study	—	—	276(28)	20(15)	—	43(42)

[1]For depth interval 200–500 m.

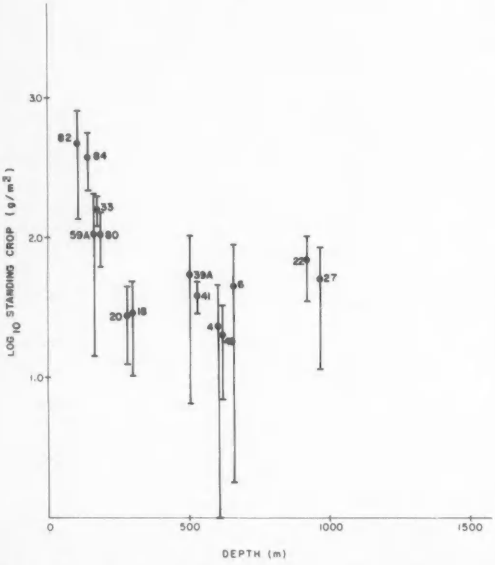

FIG. 2. Wet weight standing crop (grams per square metre) of benthic invertebrates collected in the southern Davis Strait and adjacent areas in 1977 and 1978 plotted against depth. Vertical bars represent ±1 standard deviation.

(Table 3).

The negative correlation of benthic standing crop with temperature was evidently a result of the correlation of $\log_{10}$ depth and bottom temperature ($r = 0.62$). Controlling $\log_{10}$ depth in a partial correlation analysis reduced the correlation of standing crop with bottom temperature to an insignificant level. However, controlling for depth revealed significant negative partial correlations of standing crop with fine sand content and medium sand content (−0.80 and −0.61, respectively) and positive partial correlations with sorting index, silt content, and clay content (0.60, 0.61, and 0.65, respectively). All partial correlations of standing crop with sediment characteristics, with the exception of medium sand content, were rendered insignificant when fine sand content in addition to $\log_{10}$ depth was controlled. The content of both fine and medium sand thus appears to be important in addition to depth in determining benthic macrofauna standing crop.

The multiple regression equation expressing the relationship of standing crop, depth, and fine and medium sand content was

$$y = 1401.04 - 445.14X_1 - 5.30X_2 - 10.50X_3$$

where y is standing crop (grams), X_1 is $\log_{10}$ depth (metres), and X_2 and X_3 are the arcsines of the proportion of fine sand and medium sand, respectively. Most of the variation in the data was accounted for by this regression (multiple correlation coefficient $R^2 = 0.96$).

Discussion — Standing crops of macrofauna were high relative to those observed for similar depths along most of the eastern North American continental shelf (Table 4). They exceeded those from the Scotian shelf and slope (Mills 1980), the Atlantic continental shelf and slope of the United States (Rowe et al. 1974), the Middle Atlantic Bight of the United States (Wigley et al. 1976), and Georges Bank (Wigley 1961). However, standing crops at stations 18 and 20 were similar to those observed for the same depth range in the Gulf of Maine (Rowe et al. 1975).

Davis Strait standing crops were similar, however, to those found on the southern Labrador Shelf, the Newfoundland Grand Banks, and St. Pierre, Green, Misaine, and Banquereau Banks (respectively, on the shelf south of the island of Newfoundland and on the northeastern section of the Scotian Shelf) (Nesis 1965). Those at shallowest stations in this study were similar to those observed at depths of 30–80 m in Nain Bay, Labrador (Mills 1975). The large standing crops observed by me and by Nesis (1965) probably occur because both areas lie in the productive marine subarctic. Such areas have an acknowledged elevation in water column productivity due to extensive mixing between arctic and boreal water masses (Dunbar 1968).

The negative correlation in my study of benthic macro-

invertebrate standing crop with depth is observed worldwide. It is believed that the decline follows a model of exponential decay (Rowe et al. 1974), resulting from ecological cycling of organic matter in the water column before reaching the benthos. The model is expressed as a linear relationship between $\log_{10}$ standing crop and depth. But I observed such a linear relationship only for stations shallower than about 300 m (Fig. 2). The relationship for this depth range is

$$\log_{10} \text{standing crop (g)} = 3.41 - [6.87 \times \text{depth (km)}],\ r^2 = 0.95.$$

The failure of standing crop to behave according to the model over the entire depth range in my study may be due to the involvement of factors other than depth, specifically sediment grade, in determining standing crop.

In my study, both medium and fine sand content of the sediment was important in addition to depth as negative influences on standing crop. Ellis (1960) found highest standing crops of infaunal invertebrates on silty and muddy sand and lowest on mud bottoms around northeastern Baffin Island. On the New England continental shelf and Georges Bank highest crops were observed on coarse sand (Wigley et al. 1976) and on coarse sediments such as gravels and sandy gravels (Wigley 1961), as I found at station 82. Since no definitive survey of the role of sediment type in determining standing crop exists, from my analysis I suggest that physical factors in addition to depth should be included in future models of standing crop variation.

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Silicon Contamination in Diatom Nutrient Enrichment Experiments[1]

STEPHEN J. TARAPCHAK, DAVID R. SLAVENS,[2] MICHAEL A. QUIGLEY, AND JUDITH S. TARAPCHAK[3]

NOAA, Environmental Research Laboratories, Great Lakes Environmental Research Laboratory, 2300 Washtenaw Avenue, Ann Arbor, MI 48104, USA

TARAPCHAK, S. J., D. R. SLAVENS, M. A. QUIGLEY, AND J. S. TARAPCHAK. 1983. Silicon contamination in diatom nutrient enrichment experiments. Can. J. Fish. Aquat. Sci. 40: 657–664.

Large amounts of biologically available silicon (Si) were released into solution from the walls of Pyrex glass reagent bottles and Erlenmeyer flasks during nutrient bioassay

[1]GLERL contribution No. 326.

[2]Present address: Life Chiropractic College, Marietta, GA 30080, USA.

[3]Present address: Hospital Design Office, University of Michigan, Ann Arbor, MI 48109, USA.

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experiments using Lake Michigan water. Photosynthetic rates in short-term (4–7 h) incubations and diatom growth rates and maximum yields in long-term incubations (~7 d) were affected by these extraneous Si supplies. The results of conventional nutrient enrichment bioassays performed in low-Si environments can be seriously biased unless Si contamination from glass incubation containers is avoided.

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Lors d'essais biologiques sur des nutriments avec de l'eau du lac Michigan, de fortes quantités de silice (Si) biologiquement accessibles ont été libérées dans la solution en provenance des parois des bouteilles de réactifs en pyrex et des Erlenmeyers. Ces apports externes de Si influencent les taux de photosynthèse dans les incubations à court terme (4–7 h) et les taux de croissance des diatomées et les rendements maxima dans les incubations à long terme (~7 d). Les résultats d'essais biologiques conventionnels sur les nutriments effectués dans des milieux faibles en Si peuvent être sérieusement biaisés si l'on n'élimine pas une contamination par Si des récipients d'incubation en verre.

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SILICON (Si) limitation occurs in many areas of the Great Lakes system because (1) diatoms and other Si-requiring algae are often dominant components of the phytoplankton (Vollenweider et al. 1974), (2) these organisms use Si for frustule or lorica formation (Werner 1977), and (3) Si levels are frequently too low to support optimal growth rates. Epilimnetic concentrations in lakes Ontario and Erie during summer, for example, are frequently below the detection limit of analytical methods (~30 μg Si/L) (Dobson et al. 1974) and often are ≤75 μg Si/L in Lake Michigan during July and August (Schelske 1975; Conway et al. 1977; S. J. Tarapchak, unpublished observations), whereas diatoms such as *Asterionella formosa*, *Cyclotella meneghiniana*, and *Diatoma elongatum* require 110, 40, and 42 μg Si/L, respectively, to support growth at only one-half the maximum rate (Kilham et al. 1977; Tilman and Kilham 1976).

Limitation of diatom growth in natural phytoplankton assemblages by Si is frequently assessed by performing enrichment bioassays (cf. Vollenweider 1969; Goldman 1978; Healey 1979). Subsamples of lake water are dispensed into incubation containers, injected with small volumes of sterilized nutrient solutions from glass ampoules or serum bottles, and then incubated in the containers in the lake or in an incubator. Short-term physiologic responses are measured as changes in photosynthetic rates over 4–24 h following enrichment, and long-term effects on population growth are evaluated by measuring biomass as chlorophyll *a* or by counting algal cells over a period of days. Silicon is considered to have been growth limiting under natural conditions if the response in treated subsamples is greater than that in controls (subsamples receiving no nutrients) (cf. Hamilton 1969; Storch and Dietrich 1979).

Glass containers are frequently used as incubation vessels, and nutrient solutions are commonly prepared and stored in glass ampoules or glass serum bottles. Some researchers, however, have cautioned against this practice because diatom growth may be affected by Si derived from the walls of glassware (Werner 1977; Gieskes and Van Bennekom 1973). Extraneous Si could provide an unexpected nutrient source for Si-limited algae and affect results of nutrient bioassays. For example, Si additions when diatoms are Si limited could fail to show positive responses if the amounts of contaminant Si are sufficient to produce maximum growth responses or subsamples spiked with nonlimiting nutrients could yield positive responses. There is no information in the literature on the rates and amounts of Si released from glass containers and on its biological availability, and the potential effects of extraneous Si on nutrient bioassays have not been tested. This note demonstrates for the first time that relatively large amounts of biologically available Si are rapidly released from glass containers and that this can severely bias results of conventional enrichment bioassays when phytoplankton assemblages from low Si environments are tested.

Experimental design and methods — Two conditions must be satisfied to demonstrate that extraneous Si stimulates the growth of Si-requiring algae. First, significant amounts of extraneous Si relative to lake water concentrations must be introduced into containers during the incubation period. Second, this material must be in a form available to algae. Our tests were designed (1) to quantify the amounts of extraneous Si added to subsamples when they are inoculated with nutrient solutions from serum bottles, (2) to estimate amounts of Si released from the walls of glass incubation containers, and (3) to determine the effects of extraneously released Si on growth rates of Si-requiring algae in natural assemblages and in a Si-limited diatom culture.

The amounts of Si released into solution from the walls of serum bottles could vary with preparation conditions. Some investigators presoak Pyrex glass serum bottles in strong acid, assuming that a major fraction of the Si will be removed before nutrient solutions are added; others sterilize nutrient solutions in serum bottles by autoclaving or filtration. We used a combination of these procedures to measure Si release.

Twelve 70-mL Pyrex glass serum bottles were washed in Liquinox, a phosphate-free detergent (Alconox Inc., New York), and rinsed in distilled, deionized water. Six bottles were soaked in 50% HCl for ~48 h and rinsed in distilled water. Then, all of the bottles were filled with 60 mL distilled, deionized water and sealed. Three bottles from each set were autoclaved for 30 min at 1724 kPa. Silicon was measured 48 ± 2 h later by the silicomolybdate method using plastic flasks (American Public Health Association 1975). The effects of "nutrient additions" on elevating Si concentrations in lake water were calculated by assuming that 1.0-mL aliquots from serum bottles were injected into subsamples.

Lake water experiments were performed on water collected in Lake Michigan from a depth of 4 m with a 20-L PVC Niskin bottle at an offshore (43°05′12″N, 86°25′45″W) and an inshore (43°04′24″N, 86°16′15″W) station, 15 and 4 km, respectively, west of Grand Haven, MI. The potential effects of extraneous Si on phytoplankton photosynthesis in short-term incubations were evaluated by comparing responses in glass containers with those in chemically inert flasks. Polycarbonate flasks, which do not release or sorb significant amounts of Si or trace metals (Tilman and Kilham 1976; Werner 1977), were used as controls. Two additional treatments were included. Subsamples in polycarbonate flasks were spiked with trace metals to determine if increases in photosynthetic rates could be caused by trace metal release from glass containers (cf. Carpenter and Lively 1980). Subsamples in other polycarbonate flasks were spiked with reagent Si in amounts approximating Si release from glass containers (see below). If extraneous Si from glass containers affects photosynthesis, increases in photosynthetic rates should be coincident with the release of Si into solution, rates in trace metal spiked flasks should be lower than those in glass containers, and photosynthesis in Si-spiked subsamples should approximate values measured in glass containers.

Tests were performed in previously used 125-mL reagent bottles and new 125-mL polycarbonate flasks. (Flasks were soaked sequentially for 3 d in 5 mol/L HCl, in 5 mol/L NaOH, and in distilled, deionized water before their first use.) In 1976 and 1977, tests were performed in a plexiglass chamber exposed to natural daylight and maintained within 2°C of lake water temperature at the time of sampling. In 1978, bottles were placed in an incubator maintained within 2°C of lake water temperature and exposed to ~14 000 lx. Photosynthesis was measured by injecting 74–370 kBq ($[^{14}C]NaHCO_3$ from New England Nuclear, Boston, MA) into sets of reagent bottles and polycarbonate flasks. Sets of polycarbonate flasks were injected with 200 μg Si/L (as $NaSiO_3 \cdot 9H_2O$) and with a trace metal mix (from Guillard's medium at one-half strength (Nichols 1973)) from filter-sterilized solutions prepared and stored in polyethylene containers. (An amount of 212 ± 51 (SE) μg Si/L (N = 10) was released into solution in 6 ± 0.1 h from 125-mL reagent bottles.) Photosynthesis was measured at time zero and at intervals over ~4–7 h by removing three replicate sets of bottles and flasks and filtering their entire contents (125 mL) individually through 0.45-μm Millipore filters at 39.9 kPa. Filters were processed and assayed in a Beckman (model 150) liquid scintillation counter, as described by Tarapchak et al. (1981). One set of bottles and flasks was filled with 0.45-μm Millipore filtered lake water for measurements of Si release. Containers were scrubbed in Liquinox, soaked in 5 mol/L HCl for at least 6 h, and rinsed six times in distilled, deionized water before reuse.

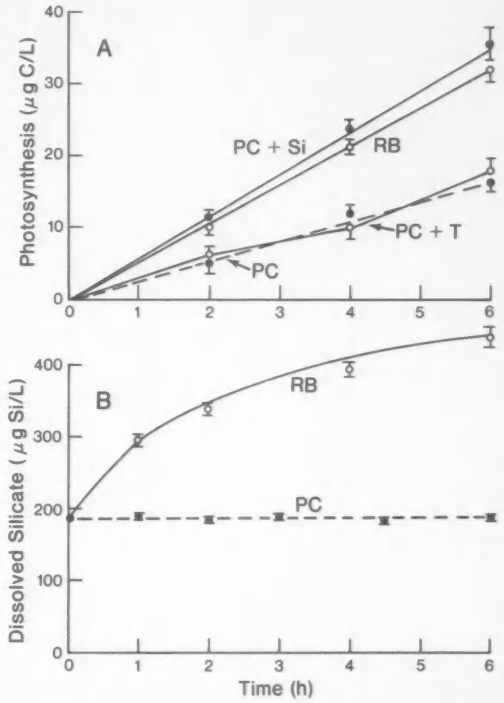

FIG. 1. Short-term bioassay using water collected from an inshore station in Lake Michigan on September 9, 1976. (A) Photosynthesis in polycarbonate control flasks (PC, broken line), glass reagent bottles (RB), and polycarbonate flasks supplemented with 200 μg Si/L (PC + Si) and trace metals (PC + T); (B) Si release from the walls of PC and RB. Vertical bars represent standard errors based on replicate measurements (N = 3) at each incubation time.

The potential effects of extraneous Si on phytoplankton growth in long-term incubations were assessed in two ways. In the first (set A), lake water was added to glass containers and polycarbonate control flasks. Contaminant effects could be difficult to demonstrate because other nutrients may quickly become limiting, causing minimal growth increases or even rapid population collapse (cf. Stoermer et al. 1971; Kalff 1971). Therefore, replicate sets of containers (set B) were inoculated with nitrate nitrogen (NO_3) (as $NaNO_3$) and phosphate phosphorus (PO_4-P) (as $NaH_2PO_4 \cdot H_2O$) at final concentrations of 144 μg N/L and 20 μg P/L. If biologically available Si is released from glass containers, growth in set A tests should be higher in glass containers than in polycarbonate controls, and/or population collapse should occur sooner in polycarbonate controls. Responses in set B experiments also should be higher in glass containers than in

TABLE 1. Ambient Si concentrations (mean of two estimates) and increases in Si concentrations (ΔSi ± SE) above ambient at the end of tests on the effects of extraneous Si on short-term photosynthetic rates using Lake Michigan water (PC, polycarbonate control flasks; PC + Si, polycarbonate flasks supplemented with Si at a final concentration of 200 μg Si/L; PC + T, polycarbonate flasks supplemented with trace metals; RB, reagent bottles).

Date	Incubation time (h)	Si (μg/L)	ΔSi (μg/L)	Photosynthesis (μg C/L)[a] PC	PC + Si	RB	PC + T	F^b
1976								
July 8	3.8	351	167±9	6.0(1)	9.4(2)	7.4(3)	—	43.2***
Aug. 12	4.9	117	209±13	24.9(1)	58.1(2)	47.6(3)	26.1(1)	23.5***
Sept. 8	4.1	328	179±11	10.3(1)	31.8(2)	30.2(2)	9.2(1)	108***
Sept. 14	4.0	468	204±15	9.7(1)	14.7(2)	14.9(2)	10.2(1)	32.3***
1977								
Aug. 17	4.0	142	178±11	13.6(1)	13.9(1)	13.3(1)	12.7(1)	0.44*
Aug. 19	4.0	66	186±16	24.5(1)	25.3(1)	23.7(1)	25.1(1)	0.22*
1978								
July 25	5.7	144	219±6	31.5(1)	31.2(1)	29.8(1)	26.3(1)	1.69*
Aug. 30	6.0	101	238±10	5.9(1)	5.8(1)	6.3(1)	—	22.1***
Sept. 19	5.7	121	234±7	7.0(1)	7.2(1)	6.9(1)	5.9(1)	1.28*
Oct. 2	6.7	400	255±11	7.1(1)	11.4(2)	10.8(2)	7.6(1)	53.4***

[a]Groups with different numbers in parentheses are statistically dissimilar at $P < 0.05$ (Newman−Kuels multiple range test) (Zar 1974).

[b]F statistic from one-way ANOVA (Zar 1974). Significance at $P > 0.10$* and $P < 0.01$***.

polycarbonate controls, and population collapse should be eliminated or diminished as sufficient supplies of NO_3 and PO_4-P are available. In both experimental sets, other polycarbonate flasks were supplemented with trace metals and Si release was measured in containers filled with filtered lake water.

Population responses were measured as changes in chlorophyll *a* in duplicate 1.0-L reagent bottles, Erlenmeyer flasks, and polycarbonate control flasks. Containers were filled with 1.0 L of water, placed in an incubator maintained within 1°C of in situ lake-water temperature, and exposed to ~14 000 lx. Si release was measured in containers filled with 1.0 L of 0.45-μm Millipore filtered water. Phytoplankton growth was expressed as maximum yield (the difference between the initial chlorophyll *a* concentration and the maximum concentration obtained during incubation) and as growth rate, k, where $k = (1/t)\ \ln\ (N/N_0)$. (N_0 = initial chlorophyll *a* concentration, N = maximum chlorophyll *a* during the exponential phase of growth, and t = time in days.) Chlorophyll *a* was measured spectrophotometrically or fluorometrically (Strickland and Parsons 1972). Procedures for cleaning containers were identical with those described above.

Silicon-limited populations of the diatom *C. meneghiniana* were used to determine whether extraneous Si is immediately available for diatom growth. The photosynthetic response of diatom populations was measured in short-term incubations in polycarbonate control flasks, glass containers, and polycarbonate flasks spiked with reagent Si. Long-term incubations were performed in the same container types without enrichment, since the culture medium provides sufficient nutrient concentrations for growth, and Si-release in both tests was measured in containers filled with nutrient medium. If extraneous Si is immediately available for growth, photosynthetic response and increases in diatom biomass should be approximately the same whether incubated in glass containers or in polycarbonate flasks spiked with Si.

The diatom was grown in batch culture through repeated transfers in Guillard's medium (Nichols 1973) in 1.0-L polycarbonate flasks at 16°C and ~14 000 lx. Prior to experiments, a 50-mL subsample from an exponentially growing culture was transferred to Guillard's medium minus Si in a 1.0-L polycarbonate flask and grown until cells were in an exponential growth phase (4−7 d). (Si concentrations at this time were below the method's detection limit (≤ ~30 μg Si/L).) Short-term effects were assessed as follows. Two-hundred-millilitre subsamples were transferred into 250-mL Erlenmeyer flasks, 250-mL polycarbonate flasks, and polycarbonate flasks supplemented with 400 μg Si/L. (An amount of 400 ± 23 (SE) μg Si/L (N = 10) was released into solution in 12 ± 0.3 h from 250-mL Erlenmeyer flasks.) Silicon release from containers was measured over time in an additional set of flasks containing Guillard's medium minus Si.

Experiments were performed by adding 100-mL subsamples of an exponentially growing culture to 900-mL of Guillard's medium in duplicate 1.0-L polycarbonate, Erlenmeyer flasks, and reagent bottles. Growth was measured by removing 25-mL subsamples from the containers and measuring optical density at 650 nm in a Fisher electrophotometer (Fisher Scientific Co.). Release of Si was measured in flasks containing filter-sterilized Guillard's medium minus Si. Procedures for cleaning containers were the same as those described above.

Results — Silica release from serum bottles — Silicon concentrations (±SE) in different sets of serum bottles were as follows: no acid soak and no autoclaving, 46.8 ± 0.00 μg Si/L; acid soak but no autoclaving, 46.8 ± 0.00 μg Si/L; no acid soak but autoclaving, 531 ± 32 μg Si/L; acid soak and

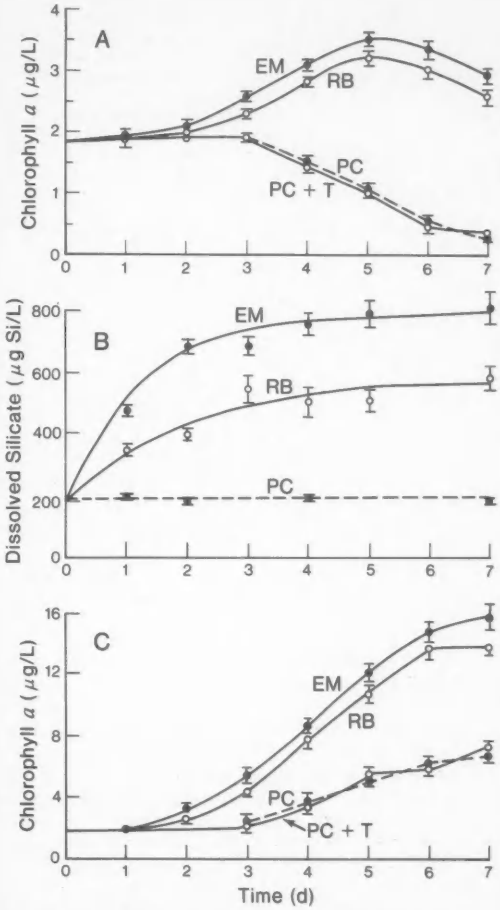

FIG. 2. Long-term bioassay using water collected from an inshore station in Lake Michigan on September 10, 1978. (A) Chlorophyll *a* concentrations in polycarbonate control flasks (PC), glass reagent bottles (RB), Erlenmeyer flasks (EM), and polycarbonate flasks supplemented with trace metals (PC + T); (B) Si release from the walls of PC and RB; (C) chlorophyll *a* concentration in EM, RB, PC, and PC + T receiving PO_4-P and NO_3-N at final concentrations of 20 μg P/L and 144 μg N/L. Vertical bars represent values measured in two containers of each type for each incubation time.

autoclaving, 559 ± 27 μg Si/L. Autoclaving resulted in the release of relatively large amounts of Si into solution; presoaking in acid did not diminish Si release. Additions of small volumes of nutrients from autoclaved bottles, however, will not significantly alter Si concentrations in Lake Michigan water (injection of 1.0 mL of solution into a 100-mL subsample at an ambient concentration of 100 μg Si/L, for example, only elevates the Si concentration by ~6 μg/L). Although such errors can be tolerated in qualitative bioassays, they can be completely eliminated by filter sterilization of solutions and storage in plastic bottles.

Lake-water tests — Results from 6 of 11 short-term tests were consistent with evidence for Si contamination: relatively large amounts of Si were released from reagent bottles into solution, photosynthetic rates for phytoplankton incubated in reagent bottles were often higher than for phytoplankton incubated in polycarbonate flasks and approximated rates detected in Si-spiked subsamples, and trace metals had no effect on photosynthesis (Fig. 1; Table 1). In most experiments showing stimulatory effects, after only 2–3 h photosynthetic rates for phytoplankton incubated in reagent bottles were statistically higher than photosynthetic rates measured in polycarbonate control flasks, suggesting that extraneous Si provides a nutrient source for diatoms or other Si-requiring algae.

Results from all long-term incubations were consistent with evidence for Si contamination: large amounts of Si were released into solution in glass containers, responses were higher for phytoplankton in glass containers than in polycarbonate control flasks, and trace metals had no effect on growth (Fig. 2; Table 2). In set A experiments, phytoplankton growth rates in glass containers were low, but positive, and population levels in polycarbonate controls usually remained constant for 2–4 d, but then collapsed. The apparent stimulatory effect of extraneous Si on growth responses was dramatic in the enriched set B incubations. Maximum phytoplankton yields and *k* often were an order of magnitude higher in glass containers than in polycarbonate controls, and populations did not collapse. A microscopic examination of subsamples after 5–7 d showed that diatoms (especially *Fragilaria*, *Synedra*, *Cyclotella*, *Stephanodiscus*, and *Nitzschia*) accounted for nearly all of the biomass increase in set A incubations and ~30–70% of the increase in set B experiments. These results indicate that, apparently, a large fraction of the Si required for growth was supplied from glass containers.

Cyclotella tests — Experiments using Si-limited cultures of *C. meneghiniana* verified that Si released from glass incubation containers directly affected diatom growth (Fig. 3). Photosynthetic rates were higher when diatoms were incubated in Erlenmeyer flasks than when incubated in polycarbonate control flasks and closely approximated photosynthetic rates of populations in Si-spiked samples (Fig. 3). Likewise, diatom growth rates were higher for populations incubated in Erlenmeyer flasks than for populations incubated in polycarbonate controls. The close correspondence between increases in photosynthetic rates and chlorophyll *a* concentrations in Erlenmeyer flasks and in Si-spiked samples showed that all, or the major fraction, of extraneous Si was readily available for growth.

Discussion and conclusions — Our results demonstrate that growth rates of Si-requiring algae in lake water were stimulated by incubation in glass containers. These effects were induced by Si and not by trace metal release from glass containers because they could be reproduced by adding Si, not trace metals, to polycarbonate flasks (Tables 1, 2; Fig. 1, 2). Additionally, experiments using *C. meneghiniana* clearly

TABLE 2. Phytoplankton response to extraneous Si during 7-d incubations in containers receiving lake water (set A) and lake water plus PO_4-P and NO_3-N (set B). Ambient Si concentrations of lake water samples are given in Table 1, and ΔSi (mean of two estimates) represents the increase in Si concentration in Erlenmeyer flasks (top row) and reagent bottles (bottom row) after 7 d. Growth responses are k (days) (top row) and maximum phytoplankton yield (bottom row) (PC, polycarbonate control flasks; EM, Erlenmeyer flasks; RB, reagent bottles; PC + T, polycarbonate flasks spiked with trace metals).

		Set A[a]					Set B[a]				
Date	ΔSi (μg/L)	PC	EM	RB	PC + T	F[b]	PC	EM	RB	PC + T	F[b]
1976											
Aug. 12	610	−0.20(1)	0.13(2)	0.11(2)	−0.18(1)	28.4***	0.08(1)	0.30(2)	0.26(2)	0.09(1)	19.4***
	473	−1.4(1)	1.8(2)	1.3(2)	−1.4(1)	118***	1.2(1)	8.3(2)	6.3(3)	1.3(1)	377***
Sept. 8	583	−0.43(1)	0.16(2)	0.13(2)	−0.39(1)	8.40**	0.07(1)	0.21(2)	0.17(2)	0.05(1)	16.6**
	481	−1.3(1)	1.6(2)	1.0(3)	−1.4(1)	314***	1.1(1)	2.1(2)	1.6(1, 2)	1.0(1)	9.69**
Sept. 14	575	−0.40(1)	0.10(2)	0.08(2)	−0.45(1)	83.7***	0.09(1)	0.26(2)	0.21(2)	0.11(1)	12.9**
	502	−1.1(1)	1.7(2)	1.1(3)	−1.1(1)	95.9***	2.4(1)	16.2(2)	11.3(3)	2.2(1)	81.6***
1977											
Aug. 17	605	−0.22(1)	0.11(2)	0.07(2)	−0.28(1)	52.1***	—	—	—	—	
	473	−0.4(1)	1.2(2)	0.5(1, 2)	−0.3(1)	15.0**	—	—	—	—	
Aug. 19	571	−0.30(1)	0.16(2)	0.12(2)	−0.23(1)	93.0***	0.08(1)	0.22(2)	0.17(1, 2)	0.11(1)	8.67**
	504	−0.5(1)	1.3(2)	0.8(3)	−0.4(1)	115***	0.6(1)	4.0(2)	3.2(2)	0.5(1)	72.3***
1978											
July 25	588	−0.38(1)	0.15(2)	0.10(2)	−0.42(1)	126***	0.06(1)	0.41(2)	0.39(2)	0.08(1)	105***
	481	−2.9(1)	2.0(2)	1.6(2)	−2.6(1)	115***	3.5(1)	25.5(2)	17.5(3)	3.4(1)	49.4***
Aug. 30	575	−0.80(1)	0.18(2)	0.12(2)	—	297***	0.05(1)	0.28(1)	0.27(1)	—	2.95*
	485	−1.5(1)	1.9(2)	1.0(2)	—	83.4***	0.5(1)	4.5(2)	2.9(3)	—	136***
Sept. 19	610	−0.61(1)	0.08(2)	0.08(2)	−0.51(1)	74.9***	0.04(1)	0.19(2)	0.10(1)	0.05(1)	24.3***
	575	−1.5(1)	0.08(2)	0.07(2)	−1.4(1)	62.1***	0.3(1)	2.8(2)	1.5(3)	0.2(1)	123***
Oct. 2	595	−0.33(1)	0.17(2)	0.12(2)	−0.30(1)	62.8***	0.16(1)	0.47(2)	0.43(2)	0.10(1)	42.9***
	475	−1.6(1)	2.1(2)	1.2(3)	−1.7(1)	81.7***	0.9(1)	19.5(2)	15.3(3)	0.8(1)	82.5***

[a]Groups with different numbers in parentheses are statistically dissimilar at $P < 0.05$ (Newman−Kuels multiple range test) (Zar 1974).
[b]F statistic from one-way ANOVA (Zar 1974). Significance at $P > 0.10$*, $P < 0.05$**, and $P < 0.01$***.

showed that all, or the major fraction, of extraneous Si was immediately available for growth. Clearly, in only 2−3 h the amounts of Si released in glass containers during lake water tests were sufficient to stimulate photosynthetic rates to levels above those measured in polycarbonate controls, and after 4 h photosynthetic rates were two- to three-fold higher than those measured in polycarbonate controls (Fig. 1; Table 1). Diatom responses in long-term incubations were even more seriously affected: k and maximum yield in containers supplemented with NO_3-N plus PO_4-P often were 5−10 times higher in glass containers than in polycarbonate controls (Table 2).

Extraneous Si can affect long-term bioassay results when water from low-Si environments is spiked with NO_3-N or PO_4-P or when Si alone is added to glass containers. For example, although nitrogen does not limit phytoplankton growth in Lake Michigan (Schelske and Stoermer 1972; Schelske et al. 1974; Schelske 1974, 1975, 1977), additions of NO_3-N often stimulated phytoplankton growth 10−25% above controls when ambient Si was ≤100 μg Si/L. This failed to occur when NO_3-N was added to subsamples in polycarbonate flasks, but the effect could be reproduced by adding NO_3-N and Si simultaneously to subsamples in polycarbonate flasks (S. J. Tarapchak, unpublished observations). This response is probably caused by an increase in nitrogen demand induced by higher growth rates of Si-requiring algae. Conversely, stimulation of diatom growth by Si additions could be masked if the amounts of contaminant Si are sufficient to meet the maximum requirements of algae; i.e. growth rates in controls would be comparable with those in Si-spiked subsamples. We repeatedly demonstrated this effect by comparing phytoplankton growth rates in glass containers, polycarbonate control containers, and polycarbonate containers spiked with Si. Maximum yields and k in polycarbonate controls frequently were 2−10 times lower than those measured in glass containers or Si-spiked polycarbonate flasks (S. J. Tarapchak, unpublished observations). Our observations, therefore, cast suspicion on the reported results of long-term nutrient enrichment bioassays in other low-Si environments in which glass incubation containers have been used.

The failure of added and/or extraneous Si to elevate photosynthetic rates in nearly one-half of the short-term tests (Fig. 1; Table 1) does not necessarily indicate Si sufficiency. Diatoms undoubtedly were Si limited as ambient Si concentrations were low and most of the samples were dominated by relatively large diatom standing crops. The absence of a stimulatory effect may be due to one or more of three physiologic characteristics of nutrient-stressed diatoms. First, some Si-limited diatoms will not take up Si in the light and require either darkness or a period of dark adaptation before uptake will occur in the light (Tessenow 1966; Werner 1977). Second, some Si-limited diatoms may respond to sudden Si additions by diverting the energy required for photosynthesis for use in Si uptake. This transient response has been demonstrated for NO_3-N and PO_4-P uptake by nutrient-deficient algae (Healey 1979) and may occur because diatoms take up

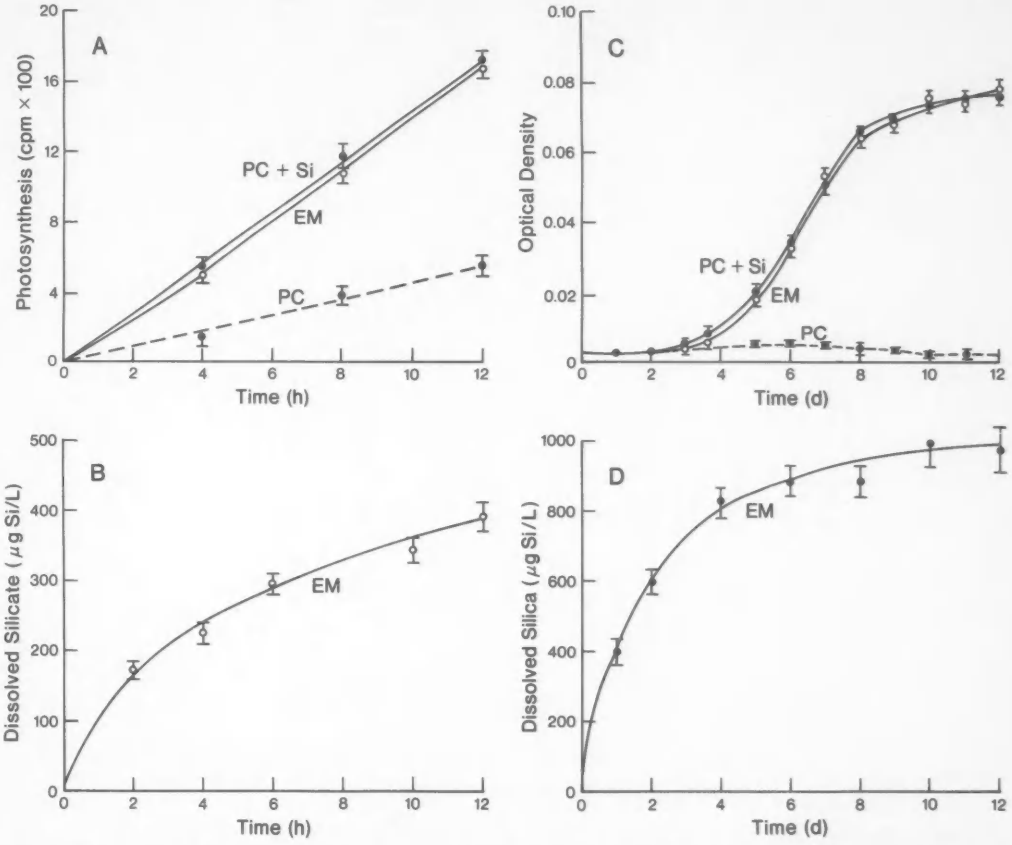

FIG. 3. Effects of extraneous Si on photosynthesis and growth of *C. meneghiniana*. (A) Photosynthesis in polycarbonate control flasks (PC), Erlenmeyer flasks (EM), and polycarbonate flasks supplemented with 400 μg Si/L (PC + Si); (B) Si release from the walls of EM during a photosynthesis experiment; (C) growth in PC control flasks, EM, and polycarbonate flasks supplemented with 800 μg Si/L (PC + Si); (D) Si release from the walls of EM. Vertical bars represent standard errors based on replicate measurements ($N = 3$) at each incubation time.

Si by active transport systems and can store Si intracellularly (Werner 1977). Third, some diatoms may be limited by other nutrients such as PO_4-P and may not take up Si at optimal rates unless that deficiency is remedied (cf. Tilman and Kilham 1976).

We could not demonstrate a depression in photosynthesis when natural diatom populations were spiked with Si but did obtain evidence for the first and third phenomena. Tests on several lake water samples showed that Si was taken up more rapidly in subsamples preincubated in the dark for 6–8 h than in subsamples continuously exposed to light, and experiments with cultured populations of *C. meneghiniana* showed that Si was taken up more rapidly by P-sufficient than by P-limited populations (S. J. Tarapchak, unpublished observations). The results of short-term bioassays, therefore, should be interpreted cautiously if photosynthetic rates in samples spiked with Si do not increase.

Our findings also have direct application to two other types of bioassays now in use. Some investigators have modified conventional short-term bioassays by adding nutrients and incubating samples for a day or more before adding [^{14}C]$NaHCO_3$ and measuring photosynthetic rates (cf. Thomas 1969; Storch and Dietrich 1979). This approach minimizes possible transient physiologic responses to sudden nutrient additions (see above) but maximizes the effects of extraneous Si on photosynthetic rates when glass containers are used. Nutrient limitation also has been assessed by using the Provisional Algal Assay Procedure (Joint Industry/Government Task Force on Eutrophication 1969). If a diatom is used as the test organism, the recommended use of Pyrex glass incubation containers could underestimate the potential importance of Si limitation because of extraneous Si contamination. Our tests mandate that chemically inert containers be used in any type of bioassay where Si-requiring algae are

important elements of algal assemblages.

Acknowledgments — E. Lynn kindly assisted in the use of computer facilities and S. Kilham generously provided cultures of *Cyclotella meneghiniana*. W. Gardner, D. Scavia, G. Fahnenstiel, and J. Kelley provided helpful comments on the manuscript.

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Ecology of Coastal Waters. A Systems Approach. *K. H. Mann. Studies in Ecology. Vol. 8. Blackwell Scientific Publications, Oxford, London/University of California Press, Berkeley/Los Angeles. x + 322 p. £10.80. $36 (cloth). $18 (paperback).*

After returning from the annual professional meetings, I usually wonder whether those of us who teach upper-division/first-year graduate courses in biological oceanography or marine ecology can be divided into those who can neither find a suitable textbook nor the time to write their own, and those who adjust or rewrite their course notes when a new book like this one appears; I wonder, too, whether professors in other fields are similar. In any case, changing course notes seems to be the faster and emotionally less draining approach, and will be worth considering in this instance.

"Coastal" in the book's title means the waters of the shelf, extending landward into estuaries and seaward to coral reefs and into the domain of coastal upwelling. Mann is writing about these regions because they are highly productive as well as utilized by man for their renewable resources, as receivers of effluents, and for their esthetic and broadly recreational purposes. His approach is synecological and process-oriented (headings of some of the 10 chapters: "Seagrass, Marsh Grass and Mangrove Systems"; "Seaweed-based Systems"; "Sediment Communities"; but also "Fish and Shellfish Production" and "Water Movement and Productivity" where estuaries, upwelling systems, and fronts in coastal waters are being treated). The book lacks the customary introductory sections, e.g., a physical description of the oceans, or a run-down of the major taxa, which are usually too cursory anyway to satisfy the upper-division/first-year graduate level readers or their instructors. Instead, introductory explanations appear when they are needed.

According to Mann, when experimenting with earlier versions, he wondered whether it would be possible to write without naming a plant or animal. In several sections, in fact, those organisms that are named seem to be used as examples rather than paradigms. The result is that Mann often writes about the forest rather than the trees, without being descriptive — another strong point of the book. (Naturally, he stresses kelp forests — moreover many of them Canadian.) The major chapters on macrophytes are actually quite specific at the same time, thus giving a profound overview, and introduce current research issues: however, chemical defences against grazing are barely mentioned, although the different balance between growth and grazing makes the kelp beds and stands of emergent macrophytes so different from the pelagic domain (p. 84, under phytoplankton). Another virtue of the book is that single-authorship not only resulted in uniformity of approach but generally also in good integration between chapters in respect to subject matter. There are a few exceptions, e.g. Steele's 1974 estimate of energy flow in the North Sea ecosystems is depicted twice (p. 122 and p. 234).

The careful reader will notice some other weaknesses: e.g. Mann uses an illustration from the literature (Fig. 1.6) that does not quantify a most important point for a marsh system, the role of detritus. Similarly, table 1.1, from Harvey's summary of 1950 for the English Channel, indicates that turnover rate of the net-collected zooplankton is the same as that of the phytoplankton; this is improbable. Figure 1.7, which is based on these data, shows bottom animals to consume more than four times as much organic matter as the benthic (and pelagic) bacteria; moreover, the figure states bacterial respiration to equal assimilation, i.e. the bacteria appear to be without production. Further, in the chapter on "Phytoplankton-based Systems," it is not obvious why section 4.7.1, on vertical migrations by zooplankton, is treated under phytoplankton consumption. (In any case, I would think that a lecturer adopting the book might want to expand on the plankton chapter, by going beyond the scope of the book and treat the open ocean as well.)

More than 650 citations refer mostly to original literature. Ironically, the index is dominated by names of organisms while the subject matter does not seem to be well covered (cf. for instance, "assimilation"; "aerobic bacteria"; "bacterial respiration").

Because of the strengths of the book, I would prefer it on the indicated instructional level over the "Fundamentals of Aquatic Ecology," edited by R. S. K. Barnes and K. H. Mann (1980, Blackwell). For the post-doctoral worker, I believe, the two chapters on macrophytes will be particularly interesting parts of the book.

KARL BANSE

School of Oceanography, WB-10
University of Washington,
Seattle, WA 98195, USA

(R443)

Mathematical Models in Biological Oceanography. *Edited by T. Platt, K. H. Mann, and R. E. Ulanowicz. Monograph on Oceanographic Methodology No. 7. UNESCO Press, Paris, France. 1981. 156 p. $12.*

This is the seventh monograph in a series on oceanographic methodology sponsored by UNESCO. The contents are a review of current modelling research, edited and largely written, by three well-known scientists. The objectives of the authors are technology transfer and dissemination of current research ideas. The text is organized into three main sections: state-of-the-art, new explorations, and research implications.

There are three themes that pervade this book. The first is stated explicitly in the guide to the contents: "For understanding biological oceanographic systems, it is necessary to have at least as much information on the fluxes as the biomasses." The others are referred to throughout: the need to "search for better understanding of processes" (which appears to supercede the need to manage stocks or ecosystems "to minimize the disruptive effects of human interference") and

the idea that "ecosystems have distinctive properties not found at lower levels in the hierarchy" of organization.

The "state-of-the-art" section nominally presents a description of the various types of models that might be used, from conceptual flow diagrams to digital ecosystem simulations. In addition there is a subsection on sensitivity analyses. However, there is clearly a bias on the part of the authors against "coupled process models." This section appears designed to discourage attempts at digital simulation with coupled process models. Certainly, such models have their limitations but they can offer profound insight into the dynamics of ecosystems and parts thereof. Most research on processes and measurement of fluxes is guided, at least implicitly, by some sort of coupled process model. Further, analyses of such models most strongly support the authors' stated contention that fluxes are as important as biomasses.

The section entitled "New explorations of ecosystem properties: a holistic view" offers a wide ranging and somewhat eclectic review of approaches. Surprisingly, a large amount of text is devoted to Isaacs' unstructured food-web model. This model appeared in the early 1970's and has had some following in the mathematical ecology literature. I am unaware of any new applications and question the extended treatment it receives. Not so surprising, given the authorship, is the attention to particle-size spectra. Sheldon's hypothesis has invoked many new ideas and continues to provide a basis for much activity current in this field. The portions on statistical mechanics and stochastic modelling are sufficient to encourage the more mathematically inclined reader. The section again does little to advance the central contention of the authors.

The title of the third section, "Implications for design of research programmes" is misleading. There is no introduction which leads into the subsections. The reference material on rates and fluxes draws primarily from the marine literature, ignoring many excellent limnological papers. The material on dimensional analysis, physical transports, and the design of programs are informative and should guide the reader into more intensive study. The unit on ecosystems under stress is weak. There are many man-induced problems to be tackled in the sea and more guidance should be given to an approach treating these problems.

The intended audience for this volume is presumed to be less-informed practitioners of biological oceanography around the world. The informed reader will easily recognize the biases of the authors, particularly against coupled process models. The uninformed reader deserves a more balanced presentation. Also there ought to be more emphasis on management-oriented modelling; today, newcomers to this field are less likely to be seeking basic understanding and more likely to be facing the task of setting harvest-quotas and devising habitat protection or restoration plans.

Although there can be little doubt that in all ecosystems studies we need to know as much, if not more, about fluxes than biomasses, this text fails to elaborate a convincing case. It fails primarily due to the bias shown toward digital simulations of coupled process models, where the need for information about fluxes is greatest.

Technically, the book is organized well and the use of words efficient. However, I can only recommend this book for its controversial bias. Reductionist and holist views and approaches must coexist. Understanding and an ability to manage ecosystems will only advance if the two viewpoints are counterbalanced.

C. K. MINNS

Department of Fisheries and Oceans
Great Lakes Fisheries Research Branch
867 Lakeshore Road
Burlington, Ont. L7R 4A6

(R462)

Books Received/Livres reçus

February/février 1983

Microbial Diseases of Fish. *Edited by R. J. Roberts. Special Publication Number 9 of the Society for General Microbiology. Academic Press, London. 1982. x + 305 p. £21.80; $40.50 (U.S.).* This book is based on a Symposium of the Pathogenicity Group of the society held at Edinburgh, 17 September 1981. Fifteen scientists have contributed to these proceedings which are of particular importance to those involved in marine and freshwater fish culture. (R472).

Crabs and their Relatives of British Columbia. *Josephine F. L. Hart. Handbook 40. British Columbia Provincial Museum, Victoria. 1982. 267 p., 102 figures and 12 color plates. $5.* Each of the 95 species of so-called crawling crabs (*Reptantia*) found in the marine waters of British Columbia is illustrated with a line drawing by the author and treated under the headings of description, color, habitat, size, range, and B.C. distribution. There are also chapters on growth, reproduction, larval development, ecology, commensalism, parasites, collecting, and economic importance. (R473)

The Effects of Air Pollution and Acid Rain on Fish, Wildlife, and their Habitats. Report 3, Introduction. *M. A. Peterson. 181 p.*; **Report 4; Lakes.** *W. Potter. 121 p.*; **Report 5, Rivers and Streams.** *W. Potter. 52 p.*; **Report 6, Forests.** *L. Borghi. 86 p.*; **Report 7, Grasslands.** *M. A. Peterson. 63 p.*; **Report 8, Arctic Tundra and Alpine Meadows.** *J. E. Olson. 29 p.*; **Report 9, Deserts and Steppes.** *E. N. Mirsky. 38 p.*; **Report 10, Urban Ecosystems.** *M. A. Peterson. 89 p.*; **Report 11, Critical Habitats of Threatened and Endangered Species.** *M. A. Peterson. 55 p. U.S. Fish and Wildlife Service, Biological Services Program, Eastern Energy and Land Use Team (FWS/OBS-80/40.3-40.11). 1982. $49 (U.S.) for nine-volume set. Available from Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402.* The reports summarize much of the available information on the effects of air pollution and acid precipitation on fish, wildlife, and their habitats. They are organized by biome types. The Introduction presents an overall view of the major air pollutants including photochemical oxidants, particulates, and acidifying air pollutants. The remaining reports of the series relate the effects of these pollutants to several major ecosystems in the United States. (R474a–i)

Tracers in the Sea. *Wallace Smith Broecker and Tsung-Hung Peng. Lamont-Doherty Geological Observatory, Columbia University, Palisades, New York 10964. 1982. 690 p.* The objective of this book is to demonstrate how the distribution of tracers in the sea and its sediments can be used to aid scientists in deciphering the operations plan and history of operation for the ocean as a chemical plant. It attempts to integrate chemical information with physical and biological and to describe how the ocean works from the point of view of a geochemist. (R475)

Stratégies d'Échantillonage en Écologie: Collection d'Écologie 17. *S. Frontier. Masson, Paris et Les Presses de l'Université Laval, Québec. 1983. 494 p. 210F.* L'ouvrage ne se veut pas un traité d'échantillonnage, ni même une mise au point exhaustive de l'état actuel des réflexions en la matière. Il reste beaucoup à réfléchir sur des problèmes théoriques et des cas concrets. La synthèse présentée devrait se traduire par une incitation à des travaux précis, sur des problèmes posés ou restant à poser. (R476)

Electricity Generation and the Ecology of Natural Waters. *T. E. Langford. Liverpool University Press, Liverpool. 1983. 342 p. £14.50 net.* In this account of the ecological effects of hydro-electricity generation, the author hopes he has been as objective as possible. He summarizes and critically reviews all major research carried out on aquatic habitats affected by the electricity industry in a number of countries. He concentrates on actual detectable and quantifiable biological effects, reviews predicted effects, and outlines future research needs. (R477)

Écologie du Plancton des Eaux continentales: Collection d'Écologie 16. *R. Pourriot, J. Capblanco, R. Champ, et J.-A. Meyer. Masson, Paris. 1982. 198 p. 184F.* Depuis le traité de B. Dussart, *Limnologie*, paru en 1966, bien peu d'ouvrages français ont été entièrement consacrés aux milieux aquatiques. C'est pourquoi, il est apparu nécessaire de faire le point sur les connaissances acquises — et sur celles qui restent à acquérir — concernant le plancton des eaux continentales en s'orientant essentiellement vers les transferts d'énergie et de matière. (R478)

ANNOUNCEMENTS/AVIS

Conference on the Biology of Marine Mammals

The Fifth Biennial Conference on the Biology of Marine Mammals will be held on November 27–December 2, 1983, in Boston, MA. This is the first time this important scientific conference regarding the conservation of and recent research on whales, dolphins, seals, and other mammals that live in the sea has been held on the East Coast. It is also the first time that it is being sponsored by The Society for Marine Mammalogy. The success of the first four conferences raised the awareness that a scientific society concerning our knowledge of whales, dolphins, and seals was needed. The New England Aquarium is acting as the Conference host; headquarters will be the new Westin Hotel in Copley Place, Boston. It is expected that nearly 1000 marine mammal scientists and conservationists from all over the United States and Canada will attend, in addition to many international researchers.

For further information on the Conference or The Society for Marine Mammalogy, all inquiries, including registration information, should be addressed to: *John H. Prescott, Conference Chairman, New England Aquarium, Central Wharf, Boston, MA 02110, USA.*

Conférence sur la biologie des mammifères marins

La cinquième Conférence biennale sur la biologie des mammifères marins se tiendra du 27 novembre au 2 décembre 1983 à Boston (MA.). C'est la première fois que cette importante réunion scientifique portant sur la conservation et les récentes recherches relatives aux baleines, dauphins, phoques et autres mammifères marins se tient sur la côte Est. C'est aussi la première fois qu'elle est sous l'égide de la *Society for Marine Mammalogy*. Le succès des quatre premières conférences a bien fait ressortir le besoin d'une société scientifique intéressée à mieux connaître les baleines, dauphins et phoques. Le *New England Aquarium* sera l'hôte de la conférence; les quartiers généraux en seront le nouvel hôtel Westin, Copley Place, Boston. En plus de nombreux chercheurs internationaux, on s'attend que près de 1 000 spécialistes et protecteurs des mammifères marins de tous les États-Unis et du Canada s'y rendront.

Pour plus ample information sur la conférence ou la *Society for Marine Mammalogy*, ainsi que sur l'enregistrement, on est prié de communiquer avec: *John H. Prescott, Président de la conférence, New England Aquarium, Central Wharf, Boston, MA 02110, É.-U.*

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Articles

Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river
D. M. Rimmer, U. Paim, and R. L. Saunders

Carotenoids as a source of pigmentation in juvenile lobsters fed a purified diet
L. R. D'Abramo, N. A. Baum, C. E. Bordner, and D. E. Conklin

An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population **D. J. Stewart, D. Weininger, D. V. Rottiers, and T. A. Edsall**

Sublethal effects of petroleum hydrocarbons on adult American lobsters (*Homarus americanus*) **J. F. Payne, J. Kiceniuk, R. Misra, G. Fletcher, and R. Thompson**

Use of variation in biological characters for the classification of anadromous rainbow smelt (*Osmerus mordax*) groups **A. Fréchet, J. J. Dodson, and H. Powles**

Mark–recapture estimates of harp seal pup (*Phoca groenlandica*) production in the northwest Atlantic **W. D. Bowen and D. E. Sergeant**

Structure–toxicity relationships for the fathead minnow, *Pimephales promelas*: narcotic industrial chemicals **G. D. Veith, D. J. Call, and L. T. Brooke**

Production estimates for Scotian Shelf copepods based on mass specific P/B ratios
M. J. Tremblay and J. C. Roff

Multispecies larval fish associations: accident or adaptation?
K. T. Frank and W. C. Leggett

Use of the *Pisces IV* submersible for zooplankton studies in coastal waters of British Columbia
G. O. Mackie and C. E. Mills

Embryo movements of Atlantic salmon (*Salmo salar*) as influenced by pH, temperature, and state of development **R. H. Peterson and D. J. Martin-Robichaud**

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